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High resolution diving behaviour of satellite tagged blue sharks under different oceanographic gradients

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O presidente do júri,

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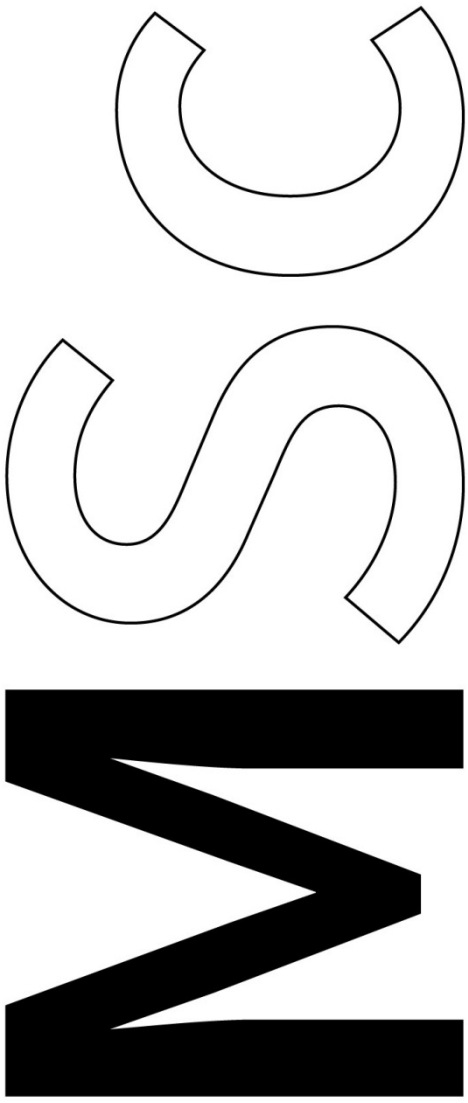

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RESUMO

A área de telemetria por satélite tem sofrido grandes progressos nos últimos anos, sendo agora possível obter dados com elevada resolução que permitem um estudo detalhado dos movimentos, padrões de actividade e comportamento de predadores pelágicos em relação a diferentes variáveis ambientais. Através de registos detalhados dos movimentos verticais dos animais marcados com transmissores, vários padrões de comportamento têm sido identificados. Adicionalmente, investigando esses padrões em relação às variáveis oceanográficas e à distribuição e abundância de presas, é possível adquirir uma maior compreensão dos aspectos que motivam esses comportamentos. Recentemente, as características dos perfis verticais, nomeadamente a forma dos mergulhos, têm sido usadas para investigar essas questões. Na maioria das espécies marinhas, os seus mergulhos podem ser classificados em diferentes tipos com base na sua forma bidimensional. É possível que estes tipos, ou determinadas características de cada tipo, representam diferentes actividades como alimentação, deslocação ou repouso. Nos peixes marinhos, em particular, dois tipos principais foram observados em várias espécies: mergulhos em forma de U e em forma de V. Em linhas gerais, pensa-se que os mergulhos em V representam procura activa de presas na coluna de água, enquanto os mergulhos em U estão relacionados com exploração de presas agregadas em profundidade. Identificar diferentes utilizações de *habitat*, por exemplo zonas de passagem e zonas de alimentação, através da análise da distribuição espacial de cada tipo de mergulho é muito importante para o reconhecimento de *habitats* vitais para a espécie, que poderão posteriormente ser úteis na delimitação de potenciais áreas de protecção marinha. Neste estudo, procedeu-se à análise de registos verticais de alta resolução de tubarões azuis monitorizados por

satélite no Atlântico Norte. Cinco tipos de mergulhos foram identificados para esta espécie, em conformidade com os tipos identificados noutras espécies pelágicas, desde tartarugas, aves e mamíferos marinhos a algumas espécies de peixes. Os tubarões azuis realizaram mergulhos em forma de U (Tipo 1) com longas durações e geralmente confinados a uma determinada profundidade, e geralmente em zonas com elevada produtividade primária, sugerindo que este tipo de mergulhos está relacionado com predação. Por outro lado, os restantes tipos de mergulho, sobretudo o Tipo 2 (forma de V), foram observados em zonas mais oligotróficas, estando assim possivelmente relacionados com deslocações ou exploração de novos *habitats*. Os indivíduos marcados com transmissores apresentaram um grande uso vertical da coluna de água, com um registo máximo de 1401 m, e grande variabilidade nos movimentos e padrões de ocupação vertical, apresentando três padrões gerais de comportamento com variação diária comuns entre indivíduos marcados em regiões diferentes do Atlântico Norte.

Palavras-chave:

Forma dos mergulhos; Mergulhos profundos; *Prionace glauca*; Utilização de habitat; Variações diárias de comportamento

ABSTRACT

Recent advances in satellite tagging technologies have provided increased resolution in studying the movements, patterns of activity and behaviour of pelagic predators in relation to different environmental features. Such accurate records of vertical movements at fine temporal resolutions have enabled the identification of variable behavioural patterns among species and individuals. In addition, by investigating diving behaviour in relation to changing oceanographic variables and to potential foraging success, we are beginning to understand why such behaviours occur at particular times and places. The characteristics of dive profiles, including dive shape, have often been useful to address such questions. For most species, dives can be classified into predefined dive types based on their two dimensional shape, and these types, or the dive characteristics within a type, may reflect activities such as foraging, travelling or resting. Concerning marine fish, two main dive types, V- and U-shaped, have been largely identified. Overall it is thought that V-shaped dives are associated with transiting/prey searching behaviour, while U-shaped profiles are related to foraging on aggregated prey. The identification of different habitat uses, namely transiting and foraging areas, by analysing the spatial distribution of the dive profiles is of great importance to the recognition of key marine habitats that can be valuable to assess potential marine protected areas. Here we analysed high-resolution dive profiles of six blue sharks *Prionace glauca* satellite tagged in the North Atlantic Ocean. Five main dive classes were identified, which have also been described among other pelagic divers, from turtles, marine birds and mammals to a few fish species. Blue sharks exhibited Type 1 dives (U-shaped) generally prolonged and confined to a certain depth layer, and predominantly in high productivity regions, suggesting that this class of dives is

related to foraging. On the other hand, the remaining classes of dives, namely Type 2 (V-shaped), were usually displayed over more oligotrophic waters, therefore more likely associated with travelling or exploration behaviours. The tagged individuals presented a very large vertical space use, with the deepest record of 1401 m, and high variability in their vertical movements and patterns of depth occupation, presenting three general patterns of diel behaviour that were common across different individuals and observed in diverse areas of the North Atlantic Ocean.

Key words:

Deep-diving; Diel patterns; Dive shape; Habitat use; *Prionace glauca*

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1. INTRODUCTION

Large pelagic fish play a key role in marine ecosystems. As apex predators, they affect prey distribution and abundance, either by direct predation or by inducing anti-predator behaviours, and therefore strongly contribute to the balance of community structure and function (Myers et al. 2007, Heithaus et al. 2008). However, a worldwide decline of large fish populations is being reported, including several shark species, and which is being mainly driven by overfishing (Baum et al. 2003, Myers et al. 2007). Even though the extent of the reported declines has been conflicting (Baum et al. 2005, Burgess et al. 2005, Pikitch et al. 2008), reductions in relative abundance of more than 50% in the past 8 to 15 years have been estimated for some species of sharks (Baum et al. 2003). Such rapid overexploitation is of particular concern and may lead to regional or ecological extinction of populations since it is unlikely that they can reproduce at a pace able to compensate for the large quantities being fished (Clarke et al. 2006), owing to their conservative life-history, namely slow growth rates, late age at maturity and low fecundity (Carrier et al. 2004).

In view of the increasing interactions between fisheries and sharks over the past century, the need of acquiring substantial knowledge of the biology, current status and ecological role of sharks has been increasingly recommended (Myers & Worm 2005, Southall et al. 2006, Pikitch et al. 2008, Kinney & Simpfendorfer 2009, ICES 2010). One very important subject to consider is the knowledge of the behavioural ecology of the species, namely regarding their spatial and temporal dynamics across different environmental gradients (Louzao et al. 2009, Mucientes et al. 2009). Until recently, the information available was very coarse and limited for most large marine species and their distribution patterns and movements, both at horizontal and vertical scales, were mostly

unknown (Sims 2010). Nevertheless, over the past 30 years there have been increasing advances on techniques for tagging and tracking several large marine predators – ranging from turtles, mammals and birds to fish (e.g. Shillinger et al. 2008, Walli et al. 2009, Pade et al. 2009, McIntyre et al. 2011, Thomson et al. 2011) – in their natural environment. These studies have usually been conducted with respect to the physical oceanographic properties that the individuals are facing, so that a better understanding of why such behaviours occur at a particular time and place can be achieved, and hence predictions of space-use patterns in response to environmental fluctuations (e.g. Heithaus et al. 2002, Sims 2010, Humphries et al. 2012).

Early tracking studies of fish species, in the 1960s and afterwards, used electronic devices that were capable of emitting or transponding sound energy, a methodology termed focal acoustic telemetry. The acoustic tags could be coupled with a wide array of sensors that transmitted data on water temperature, swimming depth, fish muscle temperature, cranial temperature, swim speed, tail beat frequency and heart rate (e.g., Carey & Scharold 1990; for an overview, see Lowe & Goldman 2001). However, with this technique only a single individual can be tracked at a time by a ship, and it has to be tracked continuously during the time period of the study (Tricas et al. 1981, Gruber et al. 1988). Therefore, the procedure becomes extremely expensive when undertaken on highly mobile species that navigate several kilometres per day (Voegeli et al. 2001). The blue shark, *Prionace glauca*, was one of the pelagic shark species tracked by acoustic telemetry in the open sea and these studies provided new insights into the patterns and range of its vertical movements. Carey & Scharold (1990) observed that the blue sharks tracked on the northeast U.S. continental shelf and slope made consistent depth excursions with a seasonal pattern. From August to March, sharks exhibited regular vertical oscillations, particularly during daylight hours, on a depth range of several hundred meters, whereas at night oscillations were smaller in amplitude and limited to the top 100 m. Remarkably, these large regular changes in depth were not seen in sharks tracked from June to July. This group remained in the upper 10 m, occasionally diving below the thermocline into colder waters at 15 m (Carey & Scharold 1990). Similar studies were carried out on other large marine predators, namely on tiger sharks, *Galeocerdo cuvier* (Holland et al. 1999, Heithaus et al. 2002) and blue marlins, *Makaira nigricans* (Block et al. 1992). In the former species, patterns of habitat use and foraging behaviour were assessed in Shark Bay, Australia (Heithaus et al. 2002) and it was observed that, although with some individual variations, tiger sharks preferred shallow seagrass habitats with abundant prey resources. Holland et al. (1999) investigated short-term movement patterns of tiger sharks close to areas of high recreational use in Hawaiian waters, and

noted that in shallow reef waters (< 300 m) they swam predominantly near to the bottom, while in open waters stayed within the mixed layer, at depths of 60 – 80 m (Holland et al. 1999). Concerning blue marlins, Block et al. (1992) observed that, in Hawaiian waters, they prefer warm near-surface depths above the thermocline, around the 26 – 27 ºC mixed layer. Overall, individuals spent half the time in the upper 10 m and never dove deeper than 200 m. Excursions below 10 m were very rare and usually lasted less than one hour (Block et al. 1992).

Although focal acoustic telemetry provides significant detail over short-term movements of each individual, the brief tracking period makes it unsuitable for the continuous capture of details over time periods greater than a few days (Carey & Robison 1981, Klimley 1993).

The first data on longer-term movements of pelagic sharks were obtained using static array monitoring, in the 1980s, and this technique has been commonly used ever since, today with modern versions of the devices (Klimley et al. 1988; for overview see Voegeli et al. 2001). Despite the fact that data-logging acoustic receivers, left on site anchored on the seabed or suspended on a buoyed line, record only presence/absence of a transmitter within its detection range, a large number of tags can be monitored simultaneously on a time span of six months to several years (depending on the number of detections received per unit time) (Sims, Wearmouth, et al. 2006). Hence, this approach allows a good data collection and monitoring on specific locations known to be aggregation sites or places to which animals usually return after long-range displacements (Simpfendorfer et al. 2002). Some examples are the monitoring of departures, arrivals and occupancy times of individual scalloped hammerhead sharks *Sphyrna lewini* along the plateau of a seamount (Klimley et al. 1988), the description of the first stages of seaward migration of wild Atlantic salmon *Salmo salar* smolts in coastal waters of eastern Canada (Lacroix & McCurdy 1996) or the tracking of vertical and horizontal movements of bocaccio (*Sebastes paucispinis*) and greenspotted (*S. chlorostictus*) rockfishes in a submarine canyon (Starr 2002), among others. Such methodology can also be useful on a conservation perspective, contributing with information that can help to delineate and properly manage Marine Protected Areas (e.g. Barnett et al. 2012)

Still in the 1980s, acoustic methods have evolved to combine radio and acoustic telemetry systems. These methods were later on applied to the investigation of detailed movements of transmitter-tagged marine animals in small areas to which individuals show some fidelity (e.g. O'Dor et al. 1998), and also to monitor fish home-range and behaviour in disturbed areas or marine reserves – in the latter to evaluate their effectiveness (e.g. Parsons et al. 2003). Despite the fact that these combined positioning

systems are not as widely used as focal acoustic telemetry or more recent archival tagging methods, they have also been helpful in revealing new movement patterns and behaviour of sharks (Sims 2010). In a study that tracked white sharks deployed off Año Nuevo Island, California, near a seal colony, it was observed that individuals spent about 40 % of their time patrolling the few kilometres monitored by the receivers, rarely venturing far from shore. Furthermore, the movements of the sharks indicated a hunting strategy independent of each other, but simultaneously their individual distributions often overlapped in the receptive field, suggesting absence of territoriality between them in this region (Klimley et al. 2001).

With recent technological advances, the early 1990s brought the development of data-loggers small enough not to hamper the swimming of the individuals but with batteries and memory sizes capable of recording and storing large amounts of high-quality data (termed archival data). They were also relatively cheap, so a large number of tags could be deployed, and in the case of species with commercial value the devices could be returned to scientists. Soon, these tags started to incorporate sensors that recorded pressure (depth), temperature and ambient light level for geolocation purposes (Arnold & Dewar 2001, Sims 2010). These tags provided more detailed temporal information, and over longer time periods, on the vertical movements of tagged individuals, and were used on several studies of sharks (e.g. dogfish *Scyliorhinus canicula*, Sims et al. 2006) and other fish species (e.g. North Sea cod *Gadus morhua*, Turner, Righton, & Metcalfe 2002). By analysing depth use at this higher resolution, over significant time spans, fairly different patterns and behaviours are sometimes detected (Sims 2010). This is the case of a study conducted on white sharks off southern Australia, where individuals showed considerable plasticity in the swimming patterns, and appeared to exhibit distinct behaviours as they moved into different habitats and travelled between them (Bruce et al. 2006). In spite of the mentioned advantages on vertical movements, geographic (horizontal) locations are quite inaccurate, as geolocation is based on light-level, sea-bed depth or tidal location methodologies. With a light-level sensor, longitude can be estimated by comparing the time of local midnight or midday with that of Greenwich, and latitude from estimates of day length. Furthermore, by comparing the recorded water temperature when the individual was at the surface with remote-sensing images of sea surface temperature, latitude estimates can be rectified and bias-reduced along the calculated longitude meridian (Teo et al. 2004, Nielsen et al. 2006). These approaches to estimate geolocation are not accurate (Arnold & Dewar 2001), therefore this tracking system only has application on species that regularly swim distances greater than the error field of the estimations. In addition, since data retrieval relies on tags being returned to scientists

through developed fisheries, data collection is unpredictable and less successful on species with little or no commercial value or protected by conservation legislation (Sims 2010).

To overcome the problems related with tags' retrieval, new satellite-linked archival tags were developed, which are able to transmit fine resolution data remotely thanks to the Argos system of satellites. Termed pop-off satellite archival transmitters (PSAT), these devices combine an Argos platform transmitter terminal (PTT) with a data-storage tag. PSATs are attached externally to the fish, release ('pop-off') from the fish at a pre-programmed time, float to the surface and transmit the data continuously to Argos satellite receivers (Block et al. 1998). This technique became a key method for tracking the movements of marine animals, namely fish (e.g., Atlantic bluefin tuna *Thunnus thynnus*, Block et al. 2001), birds (e.g., wandering albatross *Diomedea exulans*, Jouventin & Weimerskirch 1990) and mammals (e.g., sperm whale *Physeter catodon*, Watkins et al. 1999). These tags allowed successful findings in many studies, providing insights of the preferred thermal and vertical habitats occupied by the individuals under study, for example, and also of their broad scale horizontal movements. PSAT-tagged white sharks in the coast of central California underwent considerable horizontal movements to offshore areas (including one individual that travelled 3 800 km, from California to Hawaii), hence suggesting that this species is not fundamentally coastal, as previously thought (Boustany et al. 2002). However, the details provided on horizontal movements were yet very coarse and the actual trajectories of the animals still unknown. The next innovation on electronic tagging was the development of PSAT tags coupled with depth, temperature and ambient light-level sensors. With these sensors, geolocation can also be obtained using light-level, and its accuracy varies with latitude as well (e.g. North-East Atlantic, light-level geolocation errors of 50-100 km, Pade et al. 2009). Even though the Argos system is the most readily available and widely used geolocation system for telemetry studies, there are some significant disadvantages with the use of this methodology. The system can only transmit relatively small amounts of data, and the transmission time of the tags after pop-off is limited as a result of battery exhaustion. To increase rates of data retrieval, some tags (e.g. Wildlife Computers) were set to create summary data (histograms of 4-6 hours of data) that is easily transmitted remotely. Nevertheless, if the tag is retrieved the entire archival data set can be downloaded[1] (Sims 2010) and we thus acquire the records of long-term movements at fine temporal resolutions (minutes or even seconds). Such greater detail on the depth time-series recordings has enabled further developments in the field of movement ecology, providing means to thoroughly describe the movements

[1] Available at www.wildlifecomputers.com

and activity patterns of species and individuals, and then to proceed to process-based analysis and hypotheses testing that can help us to understand the motivations underlying the movements of each individual, and ideally allowing comparisons between individuals and across species (Rutz & Hays 2009, Sims 2010).

At present, satellite tags have been fundamental in identifying several behavioural patterns, such as seasonal migrations or site-fidelity (e.g. Walli et al. 2009, Pade et al. 2009), concerning horizontal movements, or diel depth changes in diving behaviour (e.g. Sims et al. 2005, Campana et al. 2011), for example, which were found to be common between several species. In terms of vertical movements, regular changes of depth use on a diel scale have been widely observed in multiple species of marine predators. The results of some studies, namely investigating the movements of swordfish *Xiphias gladius* (Sedberry & Loefer 2001, Takahashi et al. 2003), bigeye tuna *Thunnus obesus* (Dagorn et al. 2000), bigeye thresher shark *Alopias superciliosus* (Nakano et al. 2003, Weng & Block 2004) and megamouth shark *Megachasma pelagius* (Nelson et al. 1997), showed that individuals presented a pattern of diel vertical migration (DVM), clearly alternating between the occupation of warm shallow waters at night and deep cold waters during daytime. Several other shark species (e.g. blue shark, Campana et al. 2011; Carey & Scharold 1990; porbeagle shark *Lamna nasus*, Pade et al. 2009; shortfin mako *Isurus oxyrinchus*, Holts & Bedford 1993; Sepulveda et al. 2004; Pacific sleeper shark *Somniosus pacificus*, Hulbert, Sigler, & Lunsford 2006) as well as tunas (e.g. Pacific and North Atlantic Bluefin tuna, Domeier 2005; Lutcavage et al. 2000), billfishes (e.g. black marlin *Makaira indica*, Gunn, Patterson, & Pepperell 2003) and turtles (e.g. leatherback turtles *Dermochelys coriacea*, Hays et al. 2004), were not found to continuously remain at depth during the day. Instead, they exhibit regular oscillatory vertical movements, nonetheless with a higher percentage of excursions into deeper, cooler waters during the day when compared to night-time. An opposite pattern, termed reverse diel vertical migration (rDVM), has also been described in some species of sharks (porbeagle, blue and basking *Cetorhinus maximus*, Pade et al. 2009; Queiroz et al. 2012; Sims et al. 2005). As its designation suggests, when undertaking rDVM the individuals spend daylight hours near the surface and descend into deeper waters at night. Such differences in the occupation of warm surface and deep cold waters between day and night are likely due to prey movements or changes in the availability/type of prey, and have also been associated to specific oceanographic characteristics and habitats (which in fact can be influencing the availability of prey resources) (Sims, Southall, Merrett, et al. 2003, Sims et al. 2005). Indeed, shifts in diving patterns consistent with movements between different habitats and also in relation to the thermal structure of the water column have been described in

Pacific bluefin tuna *Thunnus thynnus* (Walli et al. 2009), porbeagle shark *Lamna nasus* (Pade et al. 2009) and blue sharks *Prionace glauca* (Queiroz et al. 2010, 2012), among other species. For instance, blue sharks' diving behaviour in the North-east Atlantic ranged from normal DVM and reverse DVM to a surface-oriented pattern with no diel variation, and such activity patterns occurred across different spatio-temporal scales in response to different habitat types (Queiroz et al. 2012). Intra-individual differences in vertical movements have also been documented in some studies, but to a lesser extent, possibly because high resolution data on the detailed movements undertaken by individuals is still lacking (Queiroz et al. 2010) and also because the identification and comparison of behavioural patterns is not a straightforward task (Shepard et al. 2006).

As the data collection and descriptive methods become more advanced, process-based techniques that integrate both patterns and processes are developing, aiming at testing hypotheses and developing models that can help us to understand which characteristics are driving the habitat selection and movement patterns observed in marine predators (e.g. Heithaus et al. 2002; Humphries et al. 2010; Sims, Witt, et al. 2006). Optimal searching has been one of the main issues under study in behavioural ecology. In general, all free-ranging animals are assumed to be regularly adjusting their search strategies in order to optimize the probability of encountering suitable targets, such as food or mates, and therefore a common strategy for optimizing search patterns in heterogeneous environments has possibly emerged (Stephens & Krebs 1986). Recent studies in optimal foraging theory have mainly considered search patterns described by a category of probabilistic random-walk models, termed Lévy flights (walks), which appear to be an optimal pattern when searching for patchy and low concentration prey fields on spatial scales beyond a searcher's sensory field (Viswanathan et al. 2000, Bartumeus et al. 2005). Under these specialized random walks, animal paths involve a combination of 'walk clusters' of short step length with long ballistic movements interspersed between them. Large pelagic species, which live in complex landscapes such as open ocean waters and that are capable of large displacements, have been used as a model to test for the occurrence of Lévy behaviour (Sims et al. 2008, 2012, Humphries et al. 2010, 2012). Since horizontal movement data is still subject to spatial errors or transmission gaps, such studies have used vertical movements, that are accurately recorded by satellite tags at fine temporal resolution (seconds) for long time periods (months) and for which the hypothesized probabilistic search ('blind hunting') at a horizontal scale is also expected (Sims et al. 2008). Interestingly, from the results of these studies there is strong evidence that diverse open-ocean foragers (seabirds, sea turtles, bony fish and sharks) adopt Lévy searching across natural landscapes, even though it appears that the animals keep

adjusting their optimal patterns of movement, alternating between different search motion types according to changing resource distributions (e.g. Lévy-type movements in less productive areas; Brownian-type movements when prey is abundant and not sparsely distributed) (Sims et al. 2008, 2012, Humphries et al. 2010, 2012).

Assessing habitat use of marine predators, that is, attempting to distinguish between travelling and foraging grounds, for example, has been more challenging. If detailed records of prey abundances and distribution at a landscape scale were available, it would be possible to test for correlations between particular movement patterns and prey abundance. Such a study with basking sharks, *Cetorhinus maximus*, was possible thanks to the Continuous Plankton Recorder (CPR) survey in the north Atlantic (Sims, Witt, et al. 2006). Nevertheless, that is not the case for the majority of species. Accurate feeding indices could be used instead, but these are also very difficult to obtain (Dragon et al. 2012), particularly in pelagic fish species, which spend most of the time at considerable depths. Several approaches have been developed that can be used as a proxy of these parameters. In some studies, gastric temperature data-loggers were employed to obtain the timing and when possible the estimated mass of the prey items captured (based on the time it takes for the stomach to return to normal body temperature) (Weimerskirch et al. 1994, Gunn et al. 2001, Austin et al. 2006), or it was possible to monitor the individuals and visually assess prey capture (Seminoff et al. 2006, Elliott et al. 2008). These procedures, however, are not possible to undertake in many species. The quantification of feeding events using stomach temperature sensors is only viable in ectothermic species, for which the body temperature of the ingested prey is significantly different from the predator's own body temperature (Papastamatiou 2004). Changes in gastric pH caused by feeding events could possibly be used in replacement of stomach temperature measurements, nevertheless very few studies have examined how gastric pH changes with the ingestion of prey in elasmobranchs, and some of the existing ones have yielded contrasting results (Papastamatiou 2004). The use of video recorders along with satellite tags is also impractical in pelagic species with repeated deep-diving behaviour and high swimming speeds, such as blue and mako sharks, for example.

A different approach that can give us additional insight into habitat utilization by pelagic divers has recently emerged. Some studies have been examining the two-dimensional (2D) shape of dives (i.e., depth versus time) and have clustered dives into several categories (e.g. Baechler, Beck, & Bowen 2002; Hochscheid & Godley 1999; Lesage, Hammill, & Kovacs 1999; McIntyre et al. 2011; Wilson & Block 2009). For optimally foraging predators, patterns of habitat use are assumed to reflect the distribution and quality of prey resources (Stephens & Krebs 1986, Austin et al. 2006). Therefore, it is

hypothesized that, on a vertical scale, differently shaped dives, and their frequency, persistence and characteristics, may be related to distinct activities such as foraging or travelling behaviours (Horodysky et al. 2007, Thomson et al. 2011, Dragon et al. 2012). While it is worth noting that 2D dive profiles are simplistic in their depiction of a behaviour that occurs in a 3D environment, they can still provide valuable information about the behaviour of diving animals (Halsey et al. 2007). Two fundamental dive types, U- and V-shaped, have been widely identified in several diving species, from pinnipeds (e.g. Beck et al. 2003; Halsey et al. 2007), turtles (e.g. Hochscheid & Godley 1999; Seminoff et al. 2006) and seabirds (e.g. Cook et al. 2011; Tremblay & Cherel 2000) to fish (e.g. Horodysky et al. 2007, Wilson & Block 2009). In top predators, V-shaped dives are thought to correspond to transiting or prey searching behaviours. By swimming up and down through the water column and crossing between different depth layers, animals may increase their probability of detecting olfactory cues, since odour trails essentially propagate in the ocean at a horizontal plane owing to current shear between different density layers (Carey & Scharold 1990, Pade et al. 2009). Non-foraging functions, such as predator avoidance, have also been suggested for V-shaped dives in pinnipeds (Hindell et al. 1991), but are probably not so recurrent in large pelagic predators such as sharks. On the other hand, U-shaped dives are thought to typify foraging behaviours. The time foragers spend in a specific area is assumed to be related to its prey richness (Stephens & Krebs 1986, Mori et al. 2005). Considering that this type of dives is characterized by a bottom phase of prolonged duration at a relatively constant depth, such dive types probably indicate the existence of aggregated prey patches at certain depth layers (Austin et al. 2006). Indeed, some studies in pinnipeds have reported a positive correlation between food intake and high duration of the bottom phase in U-shaped dives (Lesage et al. 1999, Baechler et al. 2002), contributing to the assumption that dive characteristics such as bottom duration or depth may reflect the distribution of prey resources. In marine turtles, U-shaped dives have also been considered benthic resting dives (e.g. Hochscheid & Godley 1999; Seminoff et al. 2006), nevertheless such function is probably related to specific physiological demands of these reptile species. Travelling and reproductive vocalizations have also been associated with this type of dives in male harbour seals, *Phoca vitulina* (Baechler et al. 2002). Other dive categories have been considered in literature studies of turtles and seals. For instance, a type designated as 'S-dives' was described by Hochscheid & Godley (1999) in green turtles, *Chelonia mydas*. This class of dives was also observed by Seminoff et al. (2006) in the same species, and by Thomson et al. (2011) in green and loggerhead turtles, *Caretta caretta*. These 'S-dives' were characterized by a steep descent to a maximum depth and a brief ascent to a specific

depth, followed by a very gradual ascent over extended time and a rapid final ascent to the surface. It has been proposed that these dives are an energy conservation strategy, where the 'stop' in the ascent represents stationary mid-water resting (Hochscheid & Godley 1999, Thomson et al. 2011). Even though there has been increasing literature focusing on the use of dive shape classification to extract information on the habitat utilization of marine predators, with recent studies including additional data (gastric temperature or video recordings, for example) to infer the reliability of such inferences (e.g. Lesage et al. 1999; Thomson et al. 2011), most studies have been conducted on air-breathing vertebrates such as pinnipeds, cetaceans, turtles and seabirds. Less consideration, however, has been given to apex predatory fish. One reason for this might be the difficulty in identifying individual dives in the time series of pelagic fish, derived from the fact that they spend most of their time, if not all, below the sea surface and do not regularly ascend to a certain depth (Wilson & Block 2009). Nevertheless, fine scale diving records collected from archival tags indicate that considerable behavioural patterns appear to exist in large pelagic fish (Wilson & Block 2009), and thus they should be equally good candidates to explore habitat utilization by marine predators using dive shape analysis.

The blue shark, *Prionace glauca* (Linnaeus, 1758), comprised in the CARCHARHINIDAE family, is perhaps one of the most interesting species in which to undertake such behavioural studies. It is an oceanic-epipelagic species, with a circumglobal distribution throughout both temperate and tropical waters (Nakano & Stevens 2008), and with an extensive vertical niche (deepest record so far is 1706 m; N. Queiroz, unpublished data). Particularly in the Atlantic Ocean, blue sharks are one of the most abundant chondrichthyan species, ranging from Newfoundland to Argentina in the west, all over Central Atlantic, and from Norway to South Africa in the east, including the Mediterranean Sea (Compagno 1984a). The blue shark feeds primarily on cephalopods, particularly squids, and small pelagic fish. Meso- and bathypelagic squid and fish species have also been reported in studies analysing stomach contents. Some invertebrates, cetaceans and seabirds have also been identified in their stomachs, but to a lesser extent (N. Queiroz, unpublished data; Clarke et al. 1996; Henderson, Flannery, & Dunne 2001; McCord & Campana 2003). Even though this species is among the most common and worldwide distributed marine predators, recent assessments report that huge numbers are captured by a wide array of fisheries, mainly as by-catch, and that it is predominant in the international shark fin trade (Baum et al. 2003, Nakano & Stevens 2008, Mejuto et al. 2009). Considering the overall abundance of blue sharks, and their moderately high reproductive rate (when compared to elasmobranchs in general), the species has been considered somewhat resilient to overfishing and endangerment (Nakano & Stevens 2008,

Camhi et al. 2009). Nevertheless, the growing evidence of population declines raises serious doubts on that view. Furthermore, having in mind that fishing pressure is not likely to diminish in the coming years, immediate action is needed to guarantee that populations of blue sharks are not depleted (Nakano & Stevens 2008, Camhi et al. 2009). For these reasons, blue sharks are among the best studied pelagic sharks concerning distribution, migrations and life history traits, particularly in the Atlantic and Pacific Oceans (Nakano & Stevens 2008). In recent years, they have also been the subject of studies intended to investigate and understand their spatial dynamics, both on horizontal and vertical scales (e.g. Humphries et al. 2010; Queiroz et al. 2012; Stevens, Bradford, & West 2010). Trans-oceanic migrations have been observed in some individuals, namely trans-equatorial movements and substantial longitudinal displacements in the Atlantic Ocean (Queiroz et al. 2005, Kohler & Turner 2008). Moreover, in the eastern North Atlantic blue sharks showed seasonal north-south movements, such as the northward migration into the western British and Irish waters (Henderson et al. 2001, Fitzmaurice et al. 2005). Blue sharks have been described performing repetitive deep-diving behaviours in several studies, and have been observed following patterns of normal or reverse diel vertical migration (DVM), but also exhibiting surface-oriented behaviours with no diel variation (Carey & Scharold 1990, Stevens et al. 2010, Queiroz et al. 2012). These patterns of vertical movements are thought to be associated with changes in the availability/type of prey, but may also be directly linked to the structure of the water column, which can influence the distribution and density of prey resources (Sims, Southall, Merrett, et al. 2003, Sims et al. 2005, Queiroz et al. 2012). Other hypothesis have been advanced to account for the oscillatory diving patterns performed by blue sharks, namely behavioural thermoregulation, where the sharks would return to the surface layer to warm up after heat loss during deep dives, or make use of repeated dives into cold waters to cool down (Carey & Scharold 1990, Klimley et al. 2002, Campana et al. 2011). However, quantitative hypothesis testing has never been employed.

The basking shark, *Cetorhinus maximus* (Gunnerus, 1765), single member of the lamniform family CETORHINIDAE, is another species for which the analysis of ecological and behavioural aspects to movement dynamics based on telemetry data has revealed interesting features. Basking sharks are the second largest fish species (reaching up to 12m) and inhabit coastal-pelagic habitats with boreal to warm-temperate waters circumglobally (Compagno 1984b). They are apex predators in a relatively short food chain (phytoplankton-zooplankton-vertebrate), and are known to, at small spatial scales, selective filter-feed on large zooplankton along oceanic and inner-shelf thermal fronts, or in areas that contain high zooplankton densities, namely of large *Calanus* spp., and minor

numbers of other smaller species (Sims & Merrett 1997, Sims & Quayle 1998). They are often seen basking in the water surface, either to feed on shallow concentrations of zooplankton or to engage in courtship and mating behaviours (e.g. close-following) (Compagno 1984b, Sims et al. 2000). Due to their massive size, they were heavily targeted for centuries for their liver oil, meat, leather and fishmeal, and also to supply the international shark fin trade (Camhi et al. 2009). To prevent a severe and irreversible depletion of populations, basking sharks are currently a protected species, listed by the Convention on International Trade in Endangered Species (CITES, Appendix II) and the Convention on Migratory Species (CMS, Appendix I and II) (and also listed in the Appendices/Annexes of some regional Conventions and Acts, such as Barcelona, Bern or Wildlife and Countryside Act of the U.K., among others) (Sims 2008, Camhi et al. 2009). Its global IUCN Red List assessment is vulnerable; however they are stated as endangered in the eastern North Atlantic and in the North Pacific (Fowler 2005). Until the past few decades, only a few simplistic studies concerning basking sharks' biology and ecology had been employed and therefore very little was known about global distribution and general activity patterns and behaviour of basking sharks (for overview, Sims 2008). Nevertheless, a significant series of studies has been undertaken in recent years (mostly in the Atlantic Ocean) that has provided considerable scientific knowledge and new information on several aspects of their behavioural ecology (e.g. Sims, Southall, Richardson, et al. 2003, Sims et al. 2005, Skomal et al. 2009). The overall movement patterns and behaviour of basking sharks over the annual cycle have not been consensual over time, mainly due to a lack of observations and studies in winter months. In the eastern North Atlantic, where most studies have been undertaken, they are frequently seen surface-feeding during summer months, which was found to be correlated with high zooplankton abundances at this time of year (Sims & Merrett 1997, Sims 1999, Sims, Southall, Merrett, et al. 2003, Southall et al. 2005). Similarly, basking sharks in the North Pacific, near British Columbia, were also often found feeding at the surface in high productive times of year (Darling & Keogh 1994). During winter, they seemed to disappear, since very rare sightings at the surface were reported (Sims, Southall, Richardson, et al. 2003). For long, it was hypothesized that this species hibernated in deep offshore waters during winter, owing to a seasonal decline in zooplankton abundance that was presumed to largely increase the energetic costs of feeding (Parker & Boeseman 1954, Sims 1999). Nevertheless, novel studies employing satellite telemetry methods, coupled with new insights on the energetic costs of feeding and threshold foraging responses of this species, have determined that they do not hibernate during winter (Sims 1999, Sims, Southall, Richardson, et al. 2003). Instead, while tracked, they performed large horizontal (up to 3400 km) and vertical

(>750 m depth) movements to utilise productive continental-shelf and shelf-edge habitats during summer, autumn and winter (Sims, Southall, Richardson, et al. 2003). It was then presumed that in the North Atlantic basking sharks present seasonal migration patterns, moving north in early summer and towards the south in late summer and autumn months, probably in response to seasonal cooling of northerly continental shelf waters (Sims, Southall, Richardson, et al. 2003, Skomal et al. 2004). Additional individuals tracked with PSAT tags in the western North Atlantic have shown the same southward migration in winter months (Skomal et al. 2009). Furthermore, some of these sharks were observed entering tropical waters along the Caribbean Islands and the South American coast of Guyana and Brazil, into the Southern Hemisphere, therefore broadening the known distribution area of basking sharks (Skomal et al. 2009). These findings support the statement of Sims (2008) that our current knowledge on the range of this species may be considerably underestimated. Most studies have indicated that basking sharks remain associated with continental shelf and shelf-edge habitats (Sims, Southall, Richardson, et al. 2003, Skomal et al. 2004, Sims, Witt, et al. 2006, Southall et al. 2006). Nevertheless, a recent study has described a transatlantic movement of a single basking shark, which covered a horizontal distance of 9589 km directly across the Atlantic from the British Isles to Newfoundland, Canada, indicating that considerable trans-oceanic migrations linking different basking shark populations might occur (Gore et al. 2008). Together with horizontal movements, considerable new information has been achieved on the vertical movements of basking sharks from archival tagging studies. Their vertical diving behaviour in the European shelf was found to be variable according to different thermal habitats (Sims et al. 2005). While in thermally stratified water masses, they exhibited a pattern of normal DVM (dusk ascent–dawn descent), but when in shallow, inner-shelf areas near thermal fronts they showed a reverse pattern (dusk descent–dawn ascent), probably due to zooplankton predator-prey interactions that induced reverse DVM of *Calanus* sp. (Sims et al. 2005). Deep-diving behaviour was also recently observed, with several mesopelagic dives being described (record depth of 1264 m), and in some cases with sharks remaining at depth for extended periods of time (weeks to months) (Gore et al. 2008, Skomal et al. 2009). A different analysis technique, signal processing (Fast Fourier Transform analysis, in this case), was also employed on the diving data of basking sharks and allowed the detection of tidal rhythms in their movements when sharks were feeding in mixed waters with strong tidal streams, in the English Channel (Shepard et al. 2006). Such studies have therefore demonstrated that basking sharks exhibit behavioural plasticity in their diving patterns, presenting some recognized patterns in particular habitats but also other apparently less structured behaviours, which might in fact be

distinctive of complex foraging strategies, such as Lévy foraging (Sims et al. 2008, Humphries et al. 2010).

Following this reasoning, the purpose of the present study was to provide a detailed description of the fine scale diving behaviour performed by blue (*Prionace glauca*) and basking (*Cetorhinus maximus*) sharks tagged with PSAT tags in the North Atlantic Ocean, based on a two-dimensional shape characterization of the dives performed by both species. Furthermore, we proposed to infer habitat use of blue and basking sharks in this region from the analysis of the spatial distribution of the observed dive types, or of specific characteristics within a type. Dive shape analyses were conducted in relation to several oceanographic features (bathymetry, temperature, water column structure and primary productivity) so that a better understanding of which factors might be influencing these sharks' behaviour could be achieved. We expect that, by combining data from two species at different trophic levels, a more robust habitat use assessment can be achieved. The identification of areas with differential habitat use, namely transiting and foraging grounds, by analysing the spatial distribution of the dive profiles can be a valuable tool to the recognition of marine habitats key to these species. Thus, the ability to identify such critical habitats, and to include data from different species of large pelagic predators, may be essential when identifying potential marine protected areas.

2. MATERIALS AND METHODS

2.1. Study area and archival tagging

Sharks of two different species, *Prionace glauca* (blue shark) and *Cetorhinus maximus* (basking shark), were tagged in the North Atlantic Ocean using pop-off satellite-linked archival transmitter (PSAT) tags (methods described in Queiroz et al. (2010) and Sims et al. (2003), for blue and basking sharks respectively). Briefly, blue sharks were tagged between July 2006 to August 2011 in three distinct areas: in the English Channel off south-western England, in the mid-Atlantic and in the North-western Atlantic; and basking sharks from May 2001 to June 2004 in two areas: the English Channel off Plymouth and in an area comprising Lower Loch Fyne and the northern Clyde Sea, in Scotland. All tags incorporated an Argos-certified transmitter with a data logger that recorded pressure, water temperature and light-level. These parameters were sampled at varying intervals (from 1 to 10 s for *P. glauca* and at 1 min intervals for *C. maximus*). All tags were programmed to detach from the shark after a designated period of days. The full archival data set was only accessible after recovery of the tags, which occurred for six blue and six basking sharks (Table 1 and Fig. 1).

Table 1. Summary data of the blue (*Prionace glauca*) and basking (*Cetorhinus maximus*) sharks from which archival tags were retrieved. Sex (F = female; M = male) is included when known. Size corresponds to fork length for blue sharks and total length for basking sharks.

ID	Species	Tagging date	Pop-up date	Days-at-liberty	Sex	Size (m)	Life stage
S1	*P. glauca*	21 Jul. 06	10 Aug. 06	20	F	1.53	Sub-adult
S2	*P. glauca*	08 Aug. 06	29 Aug. 06	21	F	1.30	Juvenile
S3	*P. glauca*	01 Aug. 07	14 Aug. 07	13	F	1.30	Juvenile
S4	*P. glauca*	21 Aug. 07	02 Nov. 07	70	F	1.50	Sub-adult
S5	*P. glauca*	25 Jun. 10	08 Jul. 10	14	M	2.00	Adult
S6	*P. glauca*	28 Aug. 11	30 Nov. 11	94	F	2.20	Adult
S7	*C. maximus*	24 May 01	30 Jul. 01	67	F	4.50	Sub-adult
S8	*C. maximus*	25 May 01	04 Dec. 01	193	-	6.00	Sub-adult
S9	*C. maximus*	31 Jul. 01	10 Feb. 02	194	-	2.50	Juvenile
S10	*C. maximus*	31 Jul. 01	20 Sep. 01	51	-	6.50	Sub-adult
S11	*C. maximus*	18 Jun. 02	25 Jun. 02	7	F	6.00	Sub-adult
S12	*C. maximus*	01 Jun. 04	03 Jul. 04	32	-	4.50	Sub-adult

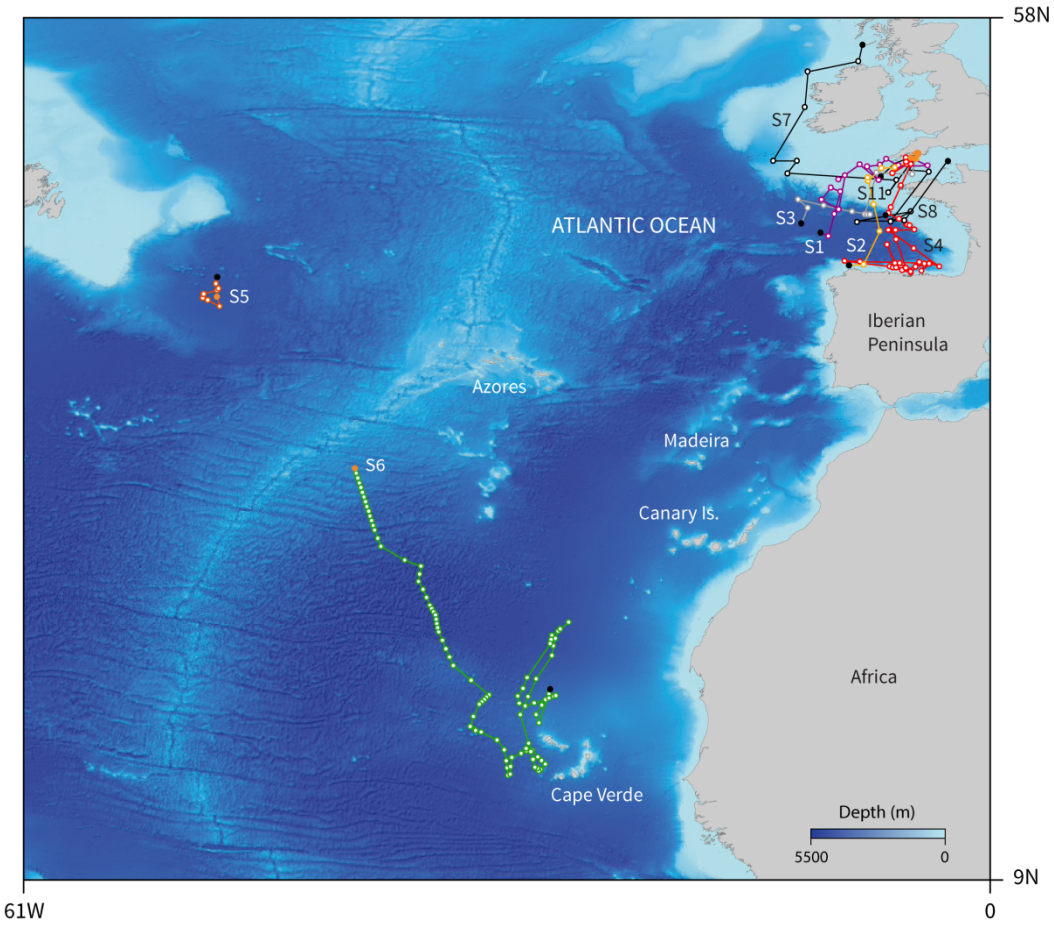

Fig. 1. Map showing the general movement patterns of six blue (S1 to S6) and three basking (S7, S8 and S11) sharks tracked with PSAT tags, overlaid on bathymetry. Bright orange circles denote tagging locations, white circles the reconstructed geolocations and black circles pop-up locations.

2.2. Horizontal movements

Blue and basking sharks' track reconstruction is described in detail in Queiroz et al. (2010) and Sims et al. (2003), and was estimated using satellite-retrieved data from each tag and also archival data after the tags were recovered. In short, daily maximal rates of change in light intensity were used to estimate the local time of midnight or midday for longitude calculations (inconsistent longitude estimates resulting from dive-induced light-intensity changes, as well as consecutive longitude estimations > 3º apart, were discarded). Latitude was then estimated along the longitude, by matching minimum and maximum water temperatures recorded by the tag to sea surface temperature (SST) values on remote-sensing images. The final estimated geolocations were then filtered for depth or swim-speed anomalies (maximum dive depth recorded for the day of each position was compared with the known seabed depth on that position; distance between consecutive positions was also analysed by a speed filter). The general horizontal movements of blue sharks (S1 to S6) and three of the basking sharks (S7, S8 and S11) are depicted in Fig. 1, with orange circles denoting tagging locations and black circles pop-off locations.

2.3. Vertical movement analysis

The time series of vertical diving movements obtained from animal-mounted archival tags was sampled at very high resolution, allowing for a detailed analysis of the sharks' diving behaviour. Such data is likely to have captured various behaviours, since the animal is constantly moving through a heterogeneous environment, namely regarding seabed depth, water temperature or prey densities. While analysing the data set as a whole may produce complex results, which will not be easily assessed and interpreted, a partitioned analysis using consistent behavioural sections may provide a clearer view on the patterns of vertical movements, which can then be linked to particular environmental features (Humphries et al. 2010). Whereas there are cases where significant shifts in the vertical time series are easily identified (by changes in patterns of vertical space use in a time depth plot, for example), in other cases these discontinuities are less clear and therefore an objective method to detect such boundaries is required. In this study, a modified version of the Split-Moving Window (SMW) analysis was employed, following Humphries et al. (2010) and Queiroz et al. (2010), and using a custom written software. To perform the analysis, a two dimensional time-at-depth (TAD) matrix, with 6 h time bins (as columns) and 10 m depth bins (as rows), was computed from the data set, by calculating the frequency of time spent at each depth class within each time bin (Fig. 2B; Fig. S. 1B, D).

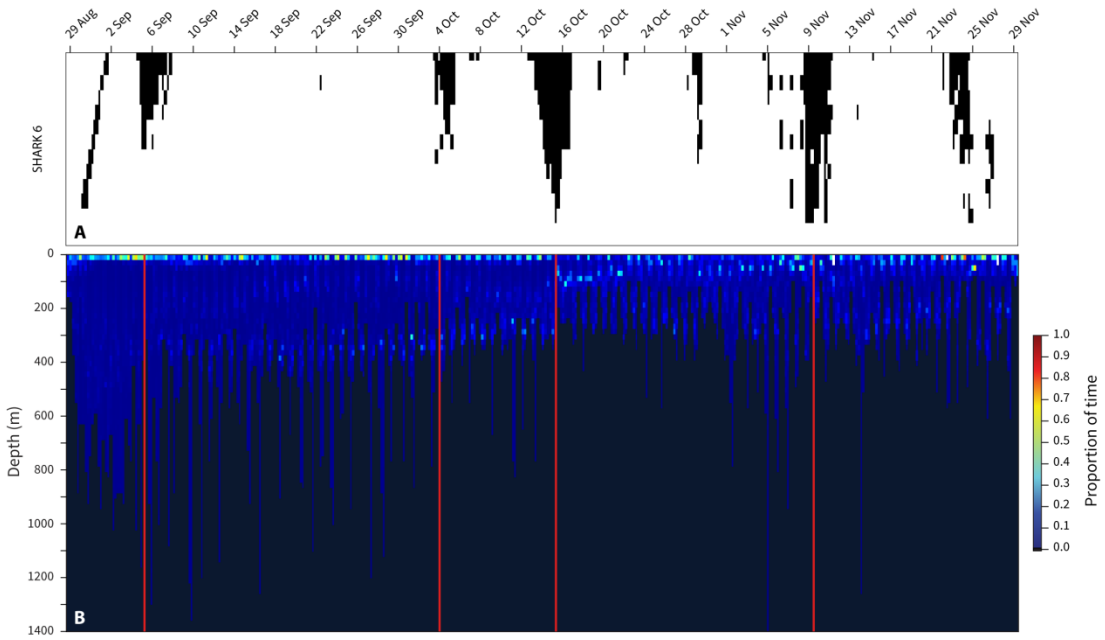

Fig. 2. Split-moving window result diagram (A) and surface plot of time-at-depth (TAD) matrix (B) of blue shark S6, tagged near the mid-Atlantic ridge. Significant discontinuities in the time series of vertical movements are depicted along the surface plot (vertical red lines).

A virtual window with a width of 6 time bins is then created and placed at the start of the TAD matrix. A multivariate measure of dissimilarity (Euclidian distance between averaged time at each depth) between the two halves of the window is calculated and assigned to the centre of the window. The window moves one step forward on the matrix and the calculation is repeated until it reaches the end of the data series. The width of the window is then incremented and the process is repeated. Statistical significance of each dissimilarity calculation is computed using a randomisation procedure (Monte-Carlo technique, with 1000 repeats with a shuffled TAD matrix). The resulting *p-values* are plotted by piling them vertically, with significant values (here, $p<0.05$) being plotted in black (Fig. 2A; Fig. S. 1A, C). Discontinuities in the patterns of vertical space use are revealed by the presence of inverted triangles that 'point' to the transition and indicate where the time series data can be objectively divided (Queiroz et al. 2010, Humphries et al. 2010). This method had already been applied on four blue (S1, S2, S3 and S4) and all six basking sharks (Queiroz et al. 2010, Humphries et al. 2010). For blue sharks, Queiroz et al. (2010) used satellite-transmitted summary data over set intervals of 4 or 6 h. In addition to this relatively low resolution, such data often has gaps due to the limited bandwidth of the Argos satellite relay system. Considering the increased resolution of the archival data set, the SMW analysis was employed in this study on all the blue sharks, to assess if new

behavioural sections were detected in sharks S1, S2, S3 and S4 and to detect sections in the additional individuals, for which data was only now analysed. The vertical movements performed by the blue sharks were complex and for this reason the results of the Split-Moving Window method were not always 'clean' and many dissimilarities were detected for some of the sharks (ex: Fig. 2A), in line with the results of Humphries et al. (2010). Following their methodology, the smaller discontinuities (shorter duration or extension over only a few window sizes), were ignored since they do not represent a persistent transition. The number of behavioural phases, and respective duration in days, detected for each shark and that will be referred to in the following sections of the work, are given in Table 2 (starting and ending dates in Table S. 1, supplementary information). Only for shark S2 our results differed from those of Queiroz et al. (2010). They had detected two behavioural sections, while we identified four different phases (Fig. S. 1, left panel).

Table 2. Number of behavioural phases, and respective duration in days, identified for each shark using the Split-Moving Window analysis. For basking sharks (S7 to S12), sections were obtained by Humphries et al. (2010).

Shark ID	Section ID	Duration (days)
S1	SEC 1	9
	SEC 2	3
	SEC 3	8
S2	SEC 1	3
	SEC 2	4
	SEC 3	9
	SEC 4	6
S3	SEC 1	7
	SEC 2	6
S4	SEC 1	8
	SEC 2	22
	SEC 3	7
	SEC 4	9
	SEC 5	25
S5	SEC 1	7
	SEC 2	7
S6	SEC 1	7
	SEC 2	31
	SEC 3	10
	SEC 4	26
	SEC 5	20
S7	SEC 1	18
	SEC 2	19
	SEC 3	30
S8	SEC 1	36
	SEC 2	9
	SEC 3	148
S9	SEC 1	31
	SEC 2	163
S10	SEC 1	19
	SEC 2	12
	SEC 3	4
	SEC 4	4
	SEC 5	8
	SEC 6	4
S11	SEC 1	3
	SEC 2	4
S12	SEC 1	4
	SEC 2	18
	SEC 3	2
	SEC 4	8

Archival data sampled at very high resolution provided the ability to analyse the spatiotemporal patterns of vertical distribution of each individual at a very fine scale. For each behavioural section of both six blue and six basking sharks, diving data was pooled and summarized as diel frequencies of time spent at depth by hour of day. This was achieved by computing TAD matrices with 10 m depth bins and 1 h time bins for the entire section and then averaging them by each hour. The resulting matrix was then depicted in the GNU R system v.2.13.1 (R development Core Team 2011), using an interpolation function in order to obtain a smoother contour plot color-coded by proportion of time (interpolation obtained using the *interp.loess( )* function from package *tgp* (Gramacy 2007)). To investigate if there were different diving behaviours by day and night, with significant differences in depth occupation, a time-weighted average of the depth experienced on each day/night of the section was computed and tested with a non-parametric Mann-Whitney *U* test at $p = 0.05$ level of significance (performed in STATISTICA v.10, StatSoft Inc. 2011). The thermal structure of the water column for each behavioural section was assessed based on pooled temperature-at-depth plots obtained using the sharks' depth and temperature archival records. Whenever these plots where difficult to interpret (due to having too many days overlapped and/or scattered data points), temperature-at-depth profiles were computed for each day of data.

2.4. Dive profile analysis

Visualization and analyses of the time series of depth data were performed in the GNU R system v.2.13.1 (R development Core Team 2011), using both the package *diveMove* (Luque 2007) and custom written programming routines.

Before any analyses, depth data were corrected for pressure-sensor drift using the 'offset' method available in the *calibrateDepth( )* function of *diveMove*. In this procedure, a specific depth value is used to correct the entire time series. For this study, the offset value was defined for each individual as the minimum depth recorded by the sensor (Table S. 2). Some individuals presented negative depth readings, and in such cases these values were replaced by zero. Considering that for *P. glauca* the sampling interval of the data logger was variable among the individuals, the archival data series of all individuals was under sampled to 10 s. All basking sharks' data were already consistently sampled at 1 min intervals.

Following a preliminary analysis of the time-depth profiles of all individuals, dives were defined as starting when fish descended below a depth of 50 m for blue sharks and

10 m for basking sharks (in *calibrateDepth( )*, using the *dive.thr* parameter). This dive threshold was necessary since blue sharks exhibit constant ranging behaviour in the top 50m, thus their dives could start and/or end at variable depths. The threshold also avoids classifying as dives between-dive surfacing events. The next step of calibrateDepth*( )* is a partition of each dive into three phases: descent, bottom and ascent. The inflection points separating each dive phase were detected by this function using a cubic smoothing spline to model each dive independently, as well as its derivative (use of a smoothing parameter of 0.4), and by applying a critical quantile of vertical velocity threshold of 0.05 m s^{-1}. All dives were then visually reviewed before the analysis to ensure that the software settings were correctly and consistently detecting all dive phases. Since time-depth profiles at such high-resolution detailed very irregular diving movements, especially in the case of *P. glauca*, this detection of dive phases was not very successful. To overcome this issue, the data series of all individuals was then under sampled to intervals of 2 min, originating a smoother vertical profile that allowed a better identification of dive phases. Nevertheless, there were still a few misidentifications (in total, 21.2% of total dives for *P. glauca* and 6.7% for *C. maximus*), and for these cases a manual assignment of phases was performed (with the use of the *extractDive( )* function of *diveMove* to isolate the time-depth data corresponding to each individual dive).

From a primary visual examination of the two-dimensional dive time series, along with a literature review (e.g. Seminoff et al. 2006, Wilson & Block 2009, Cook et al. 2011, Thomson et al. 2011), five dive shape classes consistently performed by the sharks were defined (Fig. 3), and were afterwards visually assigned to every dive. One of the classes, herein designated as Type 4, was suggested to be reptilian-specific by Hochscheid & Godley (1999). Further studies on marine turtles have observed this class of dives (Seminoff et al. 2006, Thomson et al. 2011). To our knowledge, this type has been represented graphically in a study of elephant seals (Le Beouf & Laws 1994), but has not been labelled in literature of diving birds and mammals. Type 5 dives were not found to be described in the literature, yet since they were observed in all the individuals for both species in this study, it was considered to be a relevant class of dives that should be considered in further analyses. Since the perception of a dive's shape varies with the time scale at which it is being observed, dive profiles were always observed with a 24 h time window. The dive shape allocation was always performed by the same person, and without previous knowledge of the geolocation data associated with each dive. Type 1 (U-shaped) dives were characterized by a square or parabolic shape, with well-defined descent and ascent phases and a distinct, relatively flat bottom phase. Type 2 dives were V-shaped, with a very short time spent at the maximum depth of the dive prior to ascent.

Type 3 dives were W-shaped, considered when having 2 to 4 wiggles during the bottom phase with a depth change > 10 % of the maximum dive depth, and with a depth difference between the peaks < 20 % of the maximum dive depth. Type 4 dives comprised a steep descent and a brief initial ascent followed by a clear 'stop' in ascent (where it remained at a relatively constant depth) and a steep final ascent to the surface. Type 5 dives were the reverse of Type 4 (brief initial descent followed by a clear 'stop' and a steep final descent to the maximum depth prior to ascent). Dives that did not conform to any of these five types were assigned to a sixth class (designated as 'Other'). For basking sharks, four additional types, which were variations of Type 1 (U-shaped) dives, were decided to be considered as separate classes. Two of these, designated as Type 1A and Type 1B, were U-shaped dives that presented a bottom phase with two very distinct sections, each at a fairly constant depth, but of several meters apart from one another. Type 1A dives presented the deeper section of the bottom phase during the beginning of the bottom phase, while Type 1B dives presented the deeper part of the bottom at the end of the bottom phase. Designated as Type 1C, these dives presented a very irregular bottom phase, with a significant depth range, and most of the times of extended duration (several days). The last type of dives only found to be present in basking sharks was designated as Type 1D, and comprised U-shaped dives that began and/or ended with a V-shaped 'pseudo-dive' (not considered a discrete dive since the shark did not ascended completely while performing it).

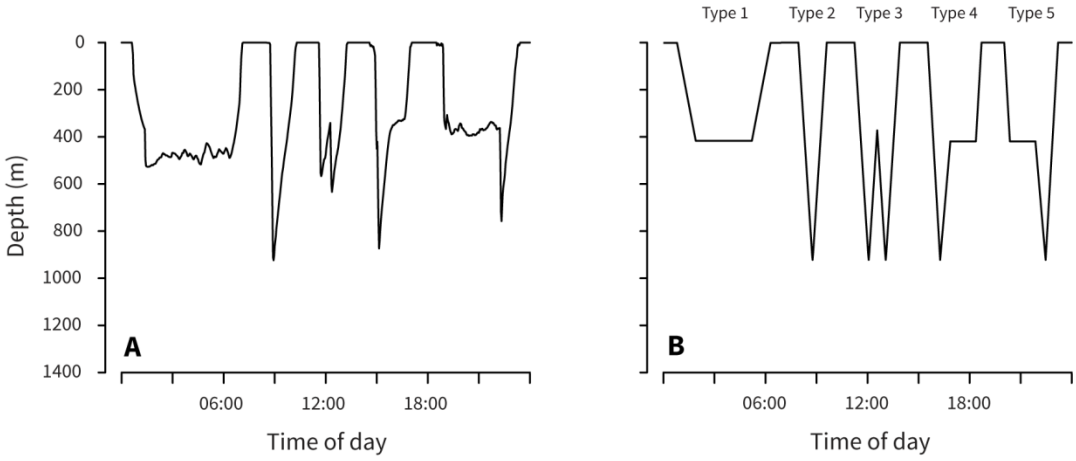

Fig. 3. Real data (A) and general (B) time-depth profiles of the five main dive shape classes considered in this study, and commonly performed by both blue and basking sharks.

There have been some studies, mostly on diving mammals, that use non-visual methods for a quantitative categorization of dives, such as cluster analysis, artificial neural networks, principal components analysis (PCA), discriminant function analysis (DFA) or random-forest algorithm (RF), among others (e.g.: Beck et al. 2003; Davis et al. 2003; McIntyre et al. 2011; Schreer & Testa 1996). However, some of these methods (namely the DFA and the RF) require a training dataset or a combination of methods to develop/validate the classification functions. These approaches are substantially more complex, requiring a lot of effort and considerable statistical knowledge to design and develop the best approach to your data. Additionally, they have only been used in air-breathing vertebrates, which perform relatively short and shallow dives, with a smooth 2D shape when compared to those of the sharks. Consequently, some researchers have preferred to employ a manual classification of dives, associated with a previous knowledge on the ecology and behavior of the study species (e.g. Hochscheid & Godley 1999, Hassrick et al. 2007, Schaefer et al. 2007, Elliott et al. 2008, Wilson & Block 2009, Cook et al. 2011). With this in mind, visual classification of dive types was considered to be the best approach in our study. Transition matrices showing the probabilities of changing from one dive type to any other were afterwards estimated for each individual, using a custom-made function under R software.

Several dive statistics were estimated using both the *diveStats( )* function of *diveMove* and supplementary R codes written for this purpose. For each dive, the following variables were considered: total dive duration; bottom phase duration; descent/ascent phase duration; mean bottom phase depth; maximum depth; percentage of intra-depth zone (IDZ), a parameter that estimates the relative depth difference between consecutive dives, and calculated as *([maximum depth – maximum depth of previous dive] / maximum depth of previous dive) × 100*, with all values considered as positive (Cook et al. 2011); mean depth of the 'stop' in ascent or descent phase, for Types 4 and 5 respectively; vertical distance travelled during descent/ascent phases; descending and ascending speeds; bottom sinuosity (measure of vertical sinuosity in the bottom phase), calculated as $BottomDistance_{observed}$ /$BottomDistance_{Euclidean}$ following Dragon et al. (2012), where $BottomDistance_{observed}$ is the total vertical distance of the bottom phase and $BottomDistance_{Euclidean}$ is the sum of the Euclidian distances from the depth at the beginning and end of the bottom phase to the maximum depth, for Types 1 and 1C; and mean depth of both the shallower and deeper sections of the bottom phase for Types 1A and 1B. These dive statistics were later analyzed taking into consideration the distinct behavioural sections defined for each individual by the Split-Moving Window method.

Given that both species presented a marked variability in diel behaviour, in some cases with contrasting depth distributions between day and night-time, the analysis of dive shape further considered a division of day and night, to allow for hypotheses testing concerning proportional occurrence of each dive type and also the estimated dive parameters on each class. In order to do so, sunrise and sunset times were defined specifically for each shark, and adjusted every five days (Table S. 3). For blue sharks, this was done by plotting light level data (recorded by the tags) for five consecutive days, and using the inflexion points of the obtained curve to estimate the hour of sunrise and sunset (Fig. 4). A five days adjustment interval was considered since light level recordings can be affected by consistent deep diving behavior, and therefore using a single day of data will not provide a sufficient way of estimating the hour of sunrise and sunset. For basking sharks, almost all light level records were of very poor quality, therefore hampering good estimations of the times of sunrise and sunset. For this reason, estimates for these sharks' time series were obtained using the Data Services of the Astronomical Applications Department of the U.S. Naval Observatory[2].

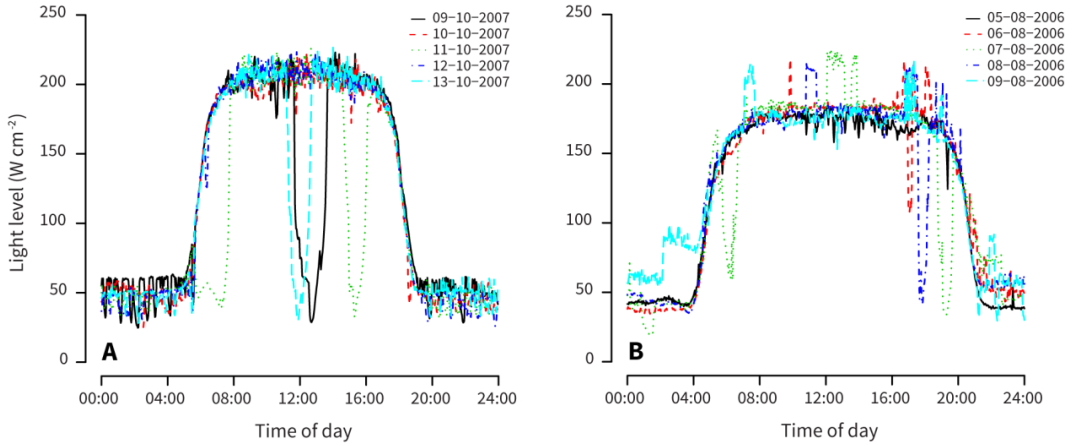

Fig. 4. Light level of five consecutive days recorded by the tags of sharks S2 (A) and S4 (B). The sunrise and sunset times for the five-day interval are then estimated using the inflexion points of the curve.

Statistical analyses were performed in R v.2.13.1 (R development Core Team 2011) and STATISTICA v.10 (StatSoft Inc. 2011), at the $p = 0.05$ level of significance. The results of the transition matrices point to the existence of some level of temporal autocorrelation between dives, suggesting that some caution is required when conducting objective hypothesis testing and statistical analyses on this topic. Since a random removal of dives

[2] Available at http://aa.usno.navy.mil/data/docs/RS_OneYear.php

to decrease this effect was not applicable as it would result in very short sample sizes, statistical tests were only applied on pooled data for all individuals. Data was tested for normality with Shapiro-Wilk test and for homogeneity of variance with Bartlett's test. A non-parametric Spearman rank correlation test was conducted to investigate if there were significant positive correlations between maximum depth and depth of the 'stop' phase for Type 4 and 5 dives, since data was not normally distributed (Shapiro-Wilk normality test , Type 4 dives: $W = 0.7332$, $p < 0.0001$; Type 5 dives: $W = 0.8579$, $p < 0.0001$). Regarding descending and ascending rates of Type 2 dives, even though the sample might not be normally distributed, the population is assumed to be (most dives probably present intermediate rates, and fewer dives very low or very high rates). Therefore, a paired t-test was employed to investigate the significance of the difference between the means of the two populations (descent and ascent rate for each dive). Non-parametric Mann-Whitney *U* tests were employed on the remaining analysis since data was not normally distributed.

The assigned dive types and the dive parameters considered more relevant for each class were then spatially represented along the sharks' tracks, using ArcGIS geographical information system, ArcMap v.10 (ESRI). A first approach was to assess the number of dives performed between the existing geolocation points, and to partition those track segments into the desired number of points, so that each dive individually, as well as its summary parameters, could be spatially represented. However, this method proved to be unreasonable since the number of dives performed by each shark was very high, hence resulting in very confusing representations. As an alternative, it was decided to obtain data points corresponding to a single day, and then aggregate dives by day. In order to do so, daily data points were interpolated from the existing geolocations when necessary (XToolsPro>Feature Conversions>Convert feature to points). A matrix was then created containing the frequency of each dive type within each day and depicted on the form of pie charts located in the corresponding latitude and longitude of that day. Nevertheless, since Type 2 dives (V-shaped) are by definition significantly shorter than the remaining ones, the use of frequencies may yield misleading results. To overcome this issue, a matrix with the proportion of time during the day the shark was spending performing each dive type was also created and represented on map. Within each dive category, there are some dive statistics that are of greater meaning than others. For Type 1 dives (U-shaped), and also Types 1A, 1B and 1C, which present a bottom phase of great proportion of total dive time, the most relevant variables are the bottom phase mean depth and duration, as well as bottom phase vertical sinuosity. For Types 2 and 3, and also Type 1D, it is the maximum depth and the rates of descent and ascent. For Types 4 and 5, the mean depth of the 'stop' phase in ascent or descent, respectively, are the most relevant features. The measured

ranges of each dive parameter were variable across sharks, therefore the summary dive statistics of all individuals, for each species separately, were combined in order to detect class breaks of each parameter's data consistent for all individuals. The obtained class breaks could then be used to plot each individual's data in particular, allowing for visual comparisons to be made among individuals. Class breaks were determined statistically by finding adjacent feature pairs between which there was a relatively large difference in data value (natural breaks), using the package *classInt* (Bivand 2011) available in the GNU R system. Afterwards, a matrix with the number of dives that fall within each parameter's class for each day was created with custom written R codes. Again, these matrices were plotted with ArcMap on the form of pie charts along each shark's track. Oceanographic gradients such as sea surface temperature (SST) and chlorophyll *a* concentration overlaid on sharks' movements were Level 3 MODIS Aqua seasonal composites (4 km grids, SST data at 4 μm nighttime) of the season and year in which sharks were tagged. For sharks S4 and S6, since they were tracked from August to November, summer and autumn seasonal composites were averaged to obtain a single map. Sea bed depth was represented using a digital bathymetry map (general bathymetric chart of the oceans GEBCO 30'' dataset).

3. RESULTS

Archival depth, temperature and light level time series records at fine temporal resolution were successfully obtained for six blue sharks tagged in the North Atlantic Ocean, of which five were females. Four were tagged off England and one near the mid-Atlantic ridge, with body-length ranging from 1.3 to 2.2 m (fork length, FL), and one male tagged in the western North-Atlantic, with 2.2 m FL.

3.1. High-resolution diving behaviour

For all individuals, the time series of vertical diving movements presented different behavioural phases, which were objectively identified using a Split-Moving Window analysis (see 'Methods'). At a spatial and oceanographic scale, the transitions between these behavioural sections were found to usually correspond to changes of physical habitat, for example bathymetry and/or thermal structure of the water column.

All four female blue sharks tagged off the English Channel (sharks S1 to S4, summer of 2006 and 2007) presented at the beginning of the track a period of on-shelf diving behaviour constrained by the bathymetry, in regions where the water column was stratified. These sharks then moved to off-shelf habitats, close to frontal features and with some degree of stratification, and exhibited much deeper (and often irregular) dives. Sharks S2 and S4 dove to a maximum depth of nearly 700 m, even when in off-shelf areas, and experienced temperatures ranging from 10.6 to 25.3 ºC (Fig. 5A; Fig. S. 2). S1 and S3 always remained above 550 m, even when not constrained by sea floor depth. The only

male, shark S5, was tracked for 14 days in the western Atlantic, near the edge of the Gulf Stream. During this short period, the shark moved across frontal waters, presenting an irregular diving behaviour to a maximum depth of 761 m, in water temperatures ranging from 6.5 to 21 ºC. Shark S6, the adult female tagged near the mid-Atlantic ridge, was tracked over 90 days, and displayed a series of very deep dives (below 1000 m) across the different behavioural sections, with a maximum record depth of 1401 m (Fig. 5B). This deep-diving behaviour was less predominant, but not bathymetrically limited, when the shark reached waters near the islands of Cape Verde, in late August. Shark S6 experienced both the warmer and coldest temperatures (5.4 – 28.1 ºC) of all blue sharks in this study.

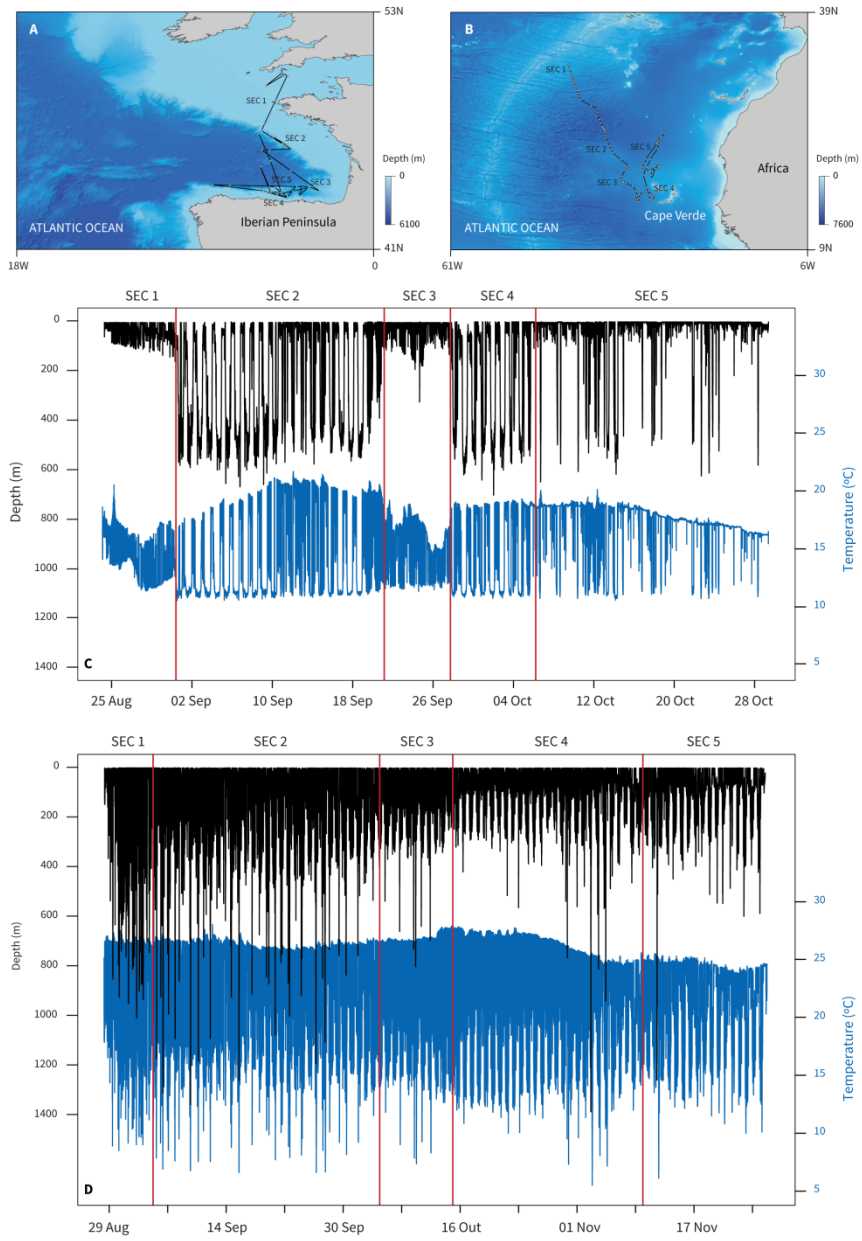

Fig. 5. Depth (black) and water temperature (blue) high-resolution profiles of sharks S4 (C) and S6 (D), tagged off the English Channel (A) and near the mid-Atlantic ridge (B), respectively. Vertical red lines correspond to significant shifts in depth occupation and where the depth time series was divided into sections ('SEC'), following the results of the Split-Moving Window analysis.

3.2. Dive shape analysis

A total of 5098 dives were identified for the six blue sharks, which performed on average 22.59 ± 10.03 dives per day (range: 9.64 – 38.27). As a result of the limitations in delineating dive phases when considering the full resolution of the archival data set, only 3225 dives were considered for subsequent dive shape analyses of *Prionace glauca* archival records (see 'Methods' section for clarification). Even so, about 21.2% of the total number of dives presented misidentified phases, and for these cases a manual assignment of phases was performed. Manual dive classification categorized dives into five general types. The mean proportion of each dive class, by frequency and also relative to the total diving time, is presented in Table 4 and in Fig. 6A. Even though a degree of inter-individual variability was noticed, a general pattern was found to occur among individuals. Type 1 (U-shaped) and Type 2 (V-shaped) dives were the most commonly performed, representing on average 68.5 % of the total number of dives. Type 2 dives alone represented 42.2 % of total dives in frequency, but since they are, by definition, shorter in duration they comprised only 12.8 % of the total dive time (whereas Type 1 dives comprised 59.6 % of dive time). The remaining dive classes (Types 3 to 5) were less frequently performed, each representing < 4 % by frequency and < 8.5 % of total dive time. It is worth noting that both sharks S2 and S6 presented a frequency of Type 5 dives of more than 5 %, which corresponded to a considerable portion of these sharks' dive time (about 34.7 and 8.9 %, respectively). About 21.9 % of the total number of dives did not conform to any of the types considered (around 10.7 % of total dive time). The observed probabilities of changing from one dive type at a given time t to another at time ($t + 1$) were not always consistent among blue sharks, but a general pattern appears to occur (Table 3). For some individuals, when exhibiting Type 1 dives it would probably perform the same type next, but in other sharks a change to a Type 2 dive was also likely to occur. When performing a Type 2 dive (V-shaped) it was most probable that it would continue displaying this class of dives for all six individuals, and if it changed it would most likely be to a Type 1 (U-shaped) dive. Types 3, 4 and 5 were almost always followed by Type 2 or Type 1 dives. Irregular dives grouped in the class 'Other' were usually performed consecutively, or followed by Type 2 and also Type 1 dives.

Table 3. Transition matrix averaged for the six blue sharks, showing the mean probabilities of changing from one dive type at a given time *t* to another at time (*t* + 1). SD is given in parenthesis.

Dive class	Type 1 (t + 1)	Type 2 (t + 1)	Type 3 (t + 1)	Type 4 (t + 1)	Type 5 (t + 1)	Other (t + 1)
Type 1 (t)	0.49 (0.12)	0.34 (0.17)	0.02 (0.02)	0.02 (0.01)	0.03 (0.02)	0.09 (0.07)
Type 2 (t)	0.19 (0.11)	0.61 (0.12)	0.06 (0.03)	0.02 (0.01)	0.03 (0.03)	0.09 (0.04)
Type 3 (t)	0.22 (0.20)	0.44 (0.31)	0.10 (0.10)	0.10 (0.09)	0.04 (0.06)	0.10 (0.11)
Type 4 (t)	0.36 (0.32)	0.33 (0.23)	0.02 (0.03)	0.11 (0.13)	0.04 (0.08)	0.14 (0.09)
Type 5 (t)	0.22 (0.26)	0.42 (0.24)	0.18 (0.40)	0.06 (0.13)	0.03 (0.04)	0.09 (0.14)
Other (t)	0.17 (0.13)	0.25 (0.14)	0.02 (0.03)	0.02 (0.02)	0.03 (0.04)	0.51 (0.23)

3.2.1. General characterization of dive types

Some characteristics of the identified dive types are illustrated in Fig. 6 and in Table 4. Type 1 (U-shaped) dives presented the longest dive durations, with some dives extending for more than 12 h, and the shortest range in maximum dive depth. Type 2 (V-shaped) dives were the shortest in total dive duration and presented a large depth range (below 1000 m), although with a mean maximum depth of 105 m (pooled from the six sharks). Types 3 to 5 presented intermediate duration and maximum depth ranges when compared to Types 1 and 2, with some Type 5 dives also extending below 1000 m (Fig. 6B). Most blue sharks' dives presented low descent and ascent rates, but there were a few dives with very high descending/ascending speeds (from 2 ms^{-1} up to about 4.1 ms^{-1}) (Fig. 6C and Fig. 6D). In general, all dive classes presented similar distributions of the relative depth difference between consecutive dives (intra-depth zone, IDZ), a parameter that allowed us to inspect if the sharks tended to dive successively to a specific depth. The distributions of percentage of IDZ were skewed to small percentages (0 – 50 %) for the five dive types (Fig. 6E). Nevertheless, a few very high IDZ values (> 500 %) were observed, with Type 2 and Type 5 dives containing the highest values (> 1000 %, to a maximum of 1904.3 %). Concerning only Type 4 and 5 dives, a significant positive correlation between the depth of the stop in ascent or descent, respectively, and the

maximum depth of the dive was found (Fig. 6F; Type 4 dives: Spearman's rank correlation coefficient $\rho = 0.88$, $p < 0.001$; Type 5: Spearman's rank correlation coefficient $\rho = 0.91$, $p < 0.001$).

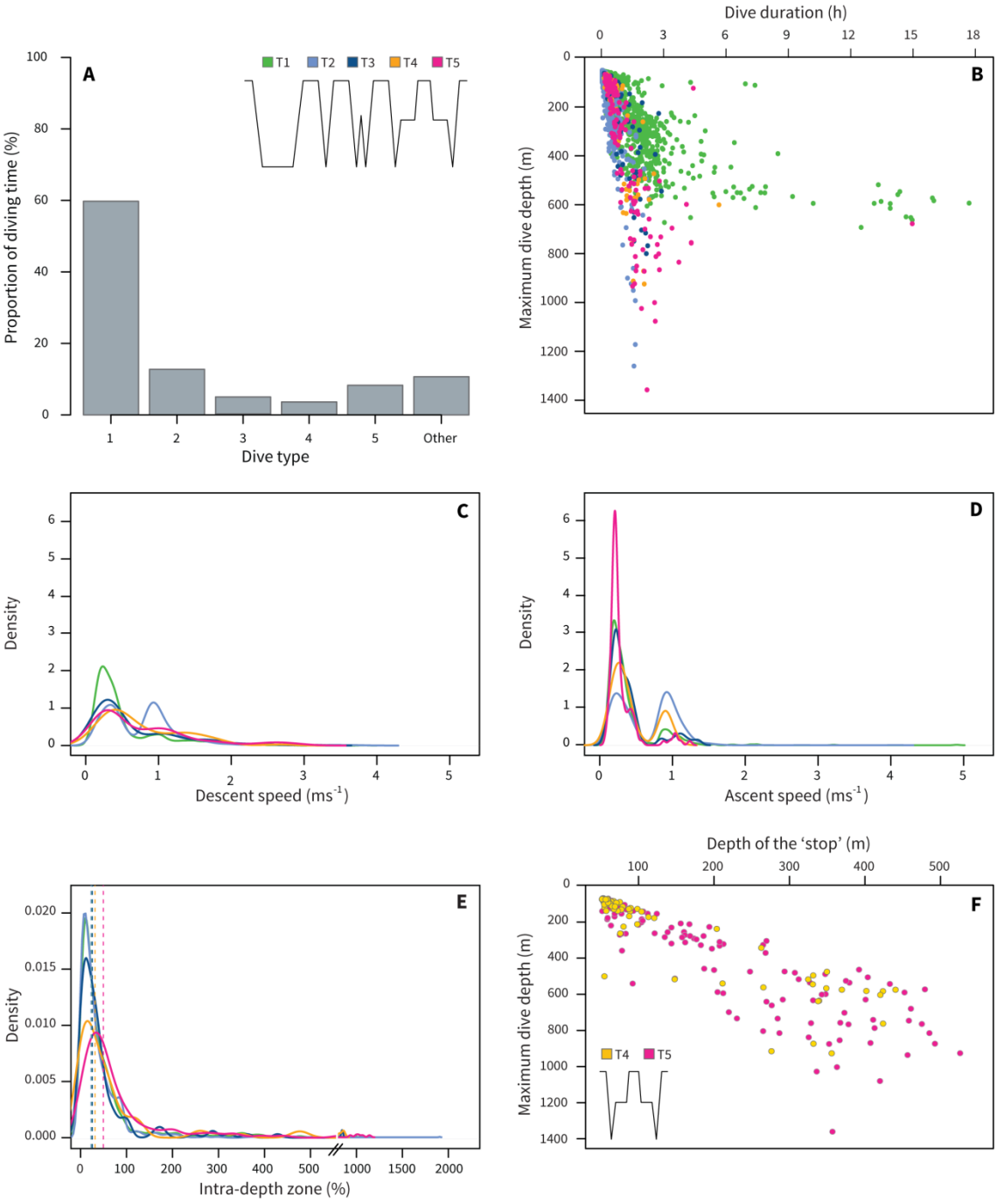

Fig. 6. General characteristics of dive classes, using pooled data of all six blue sharks. (A) Average proportion of diving time spent performing each dive type. (B) Maximum dive depth as a function of total dive duration (each point corresponds to a single dive). Density distributions of (C) descending and (D) ascending speeds. (E) Density distributions of the relative depth difference between consecutive dives, termed intra-depth zone (dashed vertical lines indicate median IDZ for each class of dives). (F) Maximum dive depth as a function of mean depth of the 'stop' phase for Type 4 and 5 dives.

Table 4. Proportional occurrence (by frequency and by total dive time) and general descriptive statistics of the five dive classes (Types 1 to 5) performed by blue sharks, *Prionace glauca*. Results are presented as mean with 1 SD in parenthesis. Dives that did not fit any of the general types were assigned to the class 'Other'.

Dive class	Type 1	Type 2	Type 3	Type 4	Type 5	Other
Frequency	0.26 (0.17)	0.42 (0.18)	0.04 (0.01)	0.03 (0.01)	0.02 (0.03)	0.22 (0.15)
Proportion of dive time	0.60 (0.19)	0.13 (0.04)	0.05 (0.04)	0.04 (0.03)	0.08 (0.13)	0.11 (0.09)
Mean dive duration (min)	132.95 (91.76)	12.41 (3.28)	47.27 (22.26)	48.67 (25.52)	66.33 (50.15)	-
Mean maximum dive depth (m)	259.78 (134.87)	105.03 (18.90)	190.25 (68.42)	221.35 (122.80)	246.66 (161.50)	-

3.2.2. Combining high resolution dive profiles with horizontal movements and oceanographic gradients

The five identified dive types and some dive parameters considered biologically more relevant for each class of dives were spatially represented along the sharks' tracks. The number of dives performed by each shark was very high, and in some cases with very short time intervals between them, therefore dives were aggregated by day and depicted along the track in the form of a pie chart (Fig. 7 and Fig. S. 3).

All five dive classes were performed by the six blue sharks and occurred generally all along the tracks, even though in some cases in very distinct frequencies. Regarding the four sharks tagged in the eastern North Atlantic, off England, S1, S3 and S4 exhibited a marked prevalence of Type 1 (U-shaped) dives at shelf and shelf-break regions, near the tidal induced and the shelf-break fronts, respectively, whereas Type 2 (V-shaped) dives were more frequently performed in off-shelf areas (Fig. 7A and Fig. S. 3A, B). S1 and S3 also performed a few Type 4 and 5 dives when in the European shelf, whereas S4 exhibited Type 4 and 5 dives all along the track. Shark S2, on the other hand, displayed several Type 2 dives when at the shelf and shelf-break regions and very few Type 1 dives along its entire track (Fig. 7B). This shark also performed a few Type 5 dives (and also Types 3 and 4, but in smaller frequencies) in off-shelf waters of the Bay of Biscay. The male blue shark tagged in the western North Atlantic (S5) had a very short and small track, located near Newfoundland and the Flemish Cap, mainly with Type 1 dives (Fig. S. 3C). Shark S6 predominantly performed Type 2 dives and also a few Type 3 dives at the beginning of the track, near the mid-Atlantic ridge, a region with low primary production (Fig. 7C).

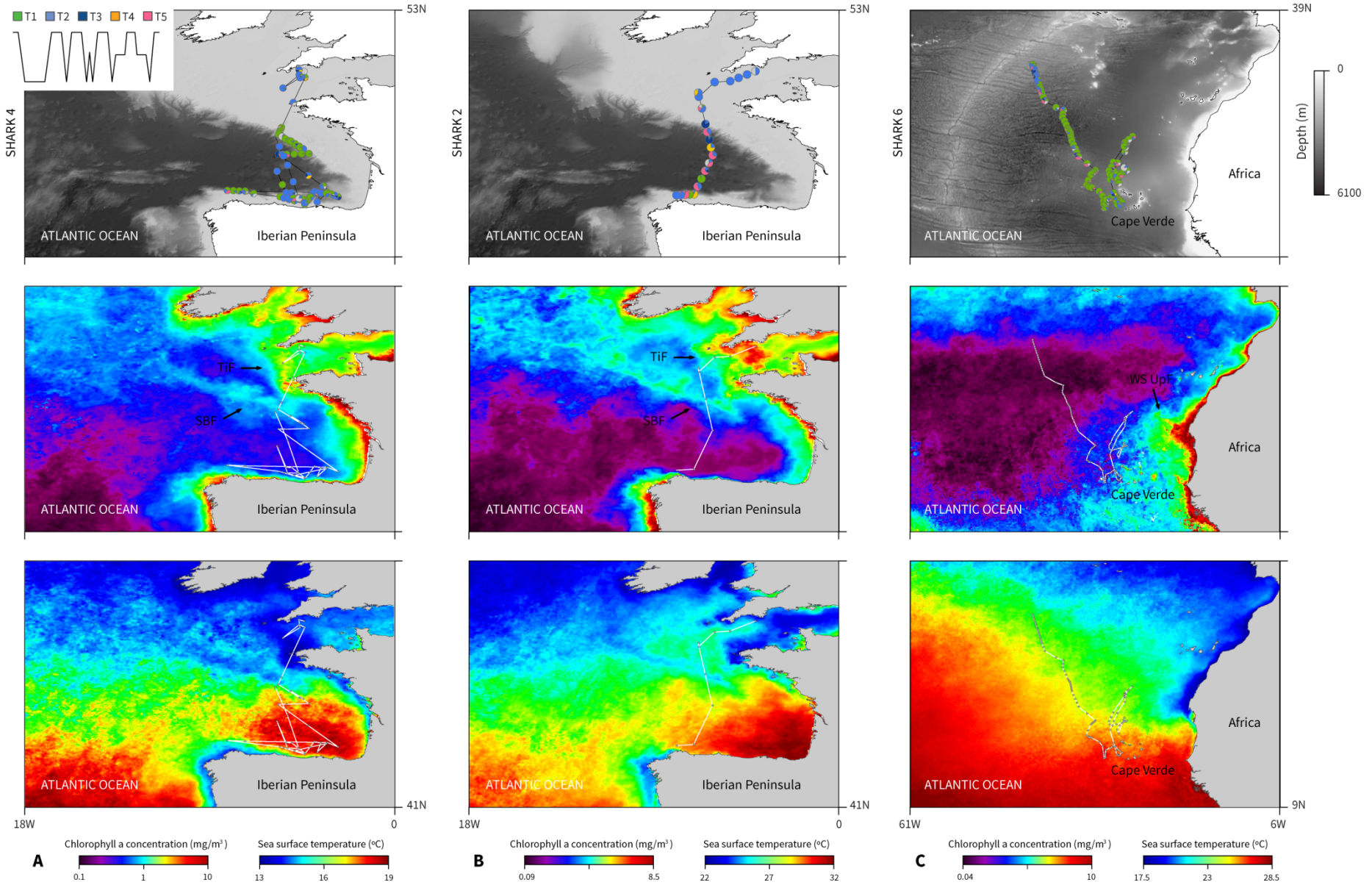

Fig. 7. Dive classes of three blue sharks represented along their horizontal movements and relation with oceanographic gradients. General movement patterns of sharks S4 (A), S2 (B) and S6 (C), with pie charts of daily proportion of time spent performing each dive type (top panels) and tracks overlaid on seasonal average of chlorophyll *a* concentration (middle panel) and sea surface temperature (bottom panels). TiF: tidal induced front; SBF: shelf-break front; WS UpF: Western Sahara upwelling front.

As it got closer to the Western Sahara upwelling front, near Cape Verde islands, the shark performed almost exclusively Type 1 dives, sometimes interspersed with other dive classes. This shark also exhibited several Type 4 and 5 dives all along its movements.

Summary parameters for each dive were also analysed in relation to the sharks' horizontal movement. Intra-depth zone (IDZ), that measures the relative difference in maximum depth between consecutive dives, was generally low in sharks S1, S2, S3 (Bay of Biscay) and S5 (Western Atlantic), with a few higher values in S2 when diving in stratified off-shelf waters. S4 presented a greater proportion of intermediate to high IDZ values, particularly when in off-shelf and shelf-edge waters. This is probably due to the marked diel variation in diving behaviour detected in these sections. Shark S6 exhibited overall low IDZ values, however with a larger proportion of intermediate to high values at the beginning of the track, near the Mid-Atlantic ridge, a region with low primary production, indicative of the irregular deep-diving behaviour displayed by this shark.

Concerning Type 1 dives (U-shaped) alone, it was considered the bottom phase mean depth, duration and vertical sinuosity (Fig. 8). In sharks S1, S2, S3 and S4 mean depth was basically constrained by the European shelf sea floor depth on the first sections of the track, and bottom phase duration was low. While S1 remained performing shallow Type 1 dives when off the shelf, mostly of short duration as well, S2 and S3 exhibited generally deeper and longer dives in stratified off-shelf/shelf-edge waters. Shark S4 performed several very deep U-shaped dives mostly when off-shelf, near the shelf break front, and in the northern Spain shelf-edge (with presence of a weak upwelling). These dives were also very extensive, in some cases with bottom phase durations of 12 to 16h. S5, in the western North Atlantic, displayed shallow dives interspersed with deeper ones and S6 intermediate Type 1 dives at the first part of the track, with an increased proportion of shallower dives when approaching the Western Sahara upwelling, near Cape Verde. In both these sharks bottom phase duration was short to intermediate. Regarding the sinuosity of the bottom phase, S1, S2 and S3 had low values across all Type 1 dives. S4 presented the higher values, but generally interspersed with low sinuosity dives, and S5 broadly intermediate values. In S6, bottom sinuosity was largely low, but with a higher frequency of high values when near Cape Verde (where Type 1 dives were predominantly performed compared to the remaining classes).

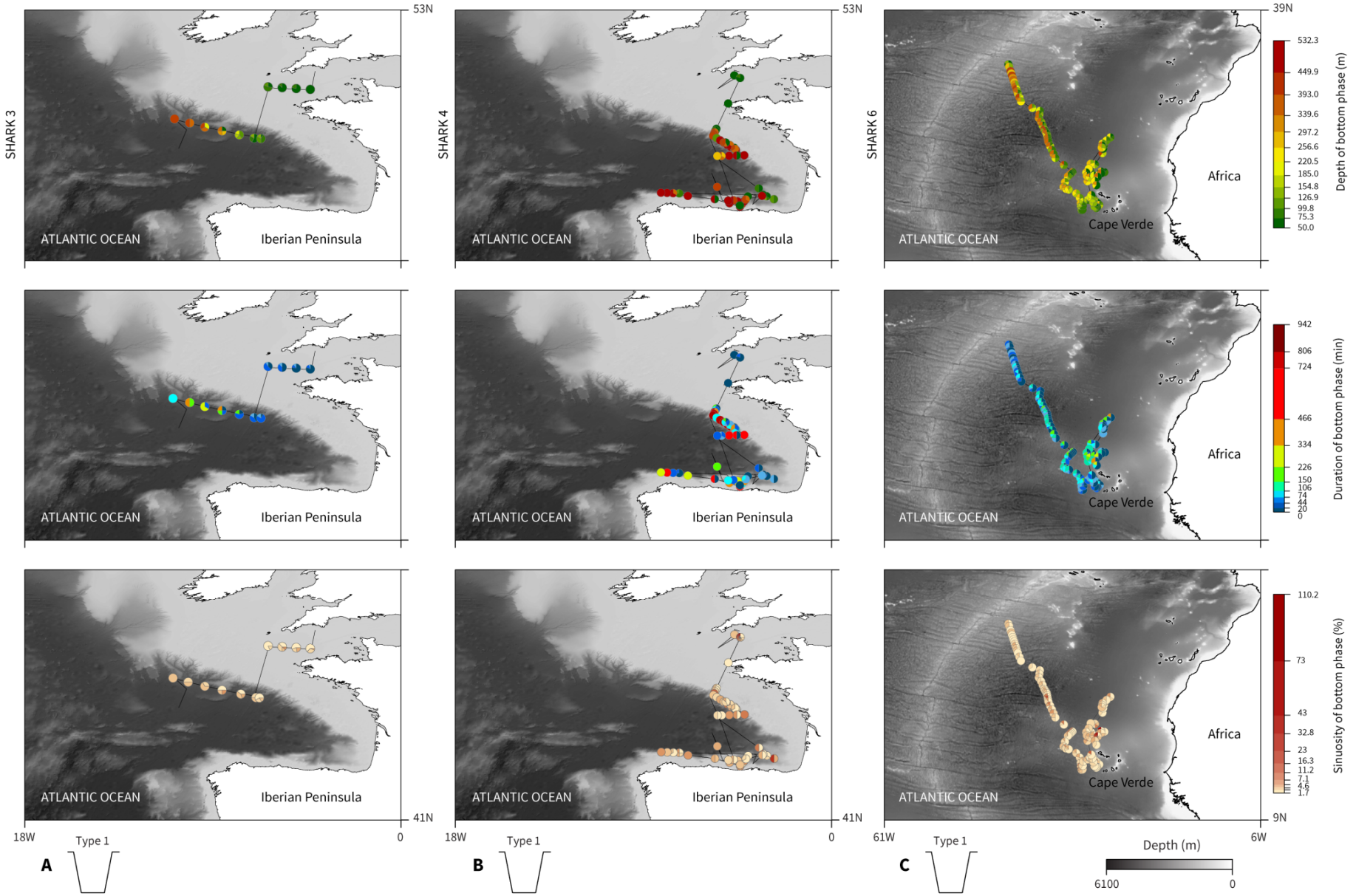

Fig. 8. Summary parameters of Type 1 (U-shaped) dives of three sharks, represented along their horizontal movements. Type 1 dives' bottom phase depth (top panel), duration (middle panel) and vertical sinuosity (bottom panel) of sharks S3 (A), S4 (B) and S6 (C), with pie charts representing the daily proportion of dives within each class of values. Class breaks in color-coded scales were statistically determined, by finding the values' boundaries between which there was a relatively large difference in data value (natural breaks).

When addressing Type 2 and 3 dives, the most relevant parameter is maximum dive depth (Fig. 9). Sharks S1, S3 and also S5 displayed shallow to intermediate Type 2 dives all along their trajectory, with Type 3 dives presenting a similar spatial distribution of maximum depth' values. S2 performed shallow Type 2 and 3 dives when on the European shelf, but several deeper dives when off the shelf (to a maximum of about 500 m in Type 2 and 700 m in Type 3 dives). Shark S4 had overall shallow dives of both classes, with some dispersed deeper dives (max. 700 m). S6 exhibited the deepest dives, particularly at the beginning of the track, near the mid-Atlantic ridge. In both types, dives were generally between 300 – 1300 m in this area, but got increasingly shallower as the shark entered the Western Sahara upwelling region, at depths similar to those performed by S1, S2 and S3 at the European shelf (but in the case of this shark dives are not bathymetrically constrained). Regarding Type 2 dives, another interesting parameter was the rate of descent/ascent for each dive (Fig. 9). In sharks S1, S3 and S4 descent and ascent rates were generally low, but with descents slightly faster than the ascent. S2 also presented descent rates higher than ascent rates, and with intermediate to high descent rates all along the track. The few Type 2 dives performed by Shark S5 had very low descent and ascent rates. Along with the deepest dives, S6 also presented the highest descent rates of all sharks, in some dives up to 4.1 ms^{-1}, all at the first section of the track, in oligotrophic waters. In these dives, the ascent was very low. When near Cape Verde, descent rates were much lower than at before, and the ascents slightly faster.

As to Types 4 and 5, the mean depth of the 'stop' phase was generally in accordance with the mean bottom phase depth of Type 1 dives (Fig. 10). In sharks S1 and S3 they were shallow, in parallel with Type 1 and 2 dives. S2 presented deeper 'stop' depths when off-shelf and near the northern Spain shelf-edge, in regions where Type 1 dives were also deeper. In S4, Type 4 dives presented a shallow 'stop' along the entire track, but in Type 5 dives it was much deeper in the regions where this shark was displaying very deep and prolonged Type 1 dives. S5 presented both shallow and deep 'stop' depths, and the same bimodality was observed in Type 1' bottom phase depths. Shark S6 had Type 4 dives with depths of the 'stop' very similar to Type 1 bottom depths, also with a clear dichotomy. At the beginning of the track both types were deep, and as the shark approached Cape Verde islands Type 1 and 4 dives were much shallower. A similar depth distribution was observed in Type 5 dives, but in the first section these dives presented 'stop' depths even deeper than Type 4 and Type 1 bottom phase depths. However, it should be noted that those Type 5 'stops' were not as deep as the Type 2 (V-shaped) dives occurring in that same area.

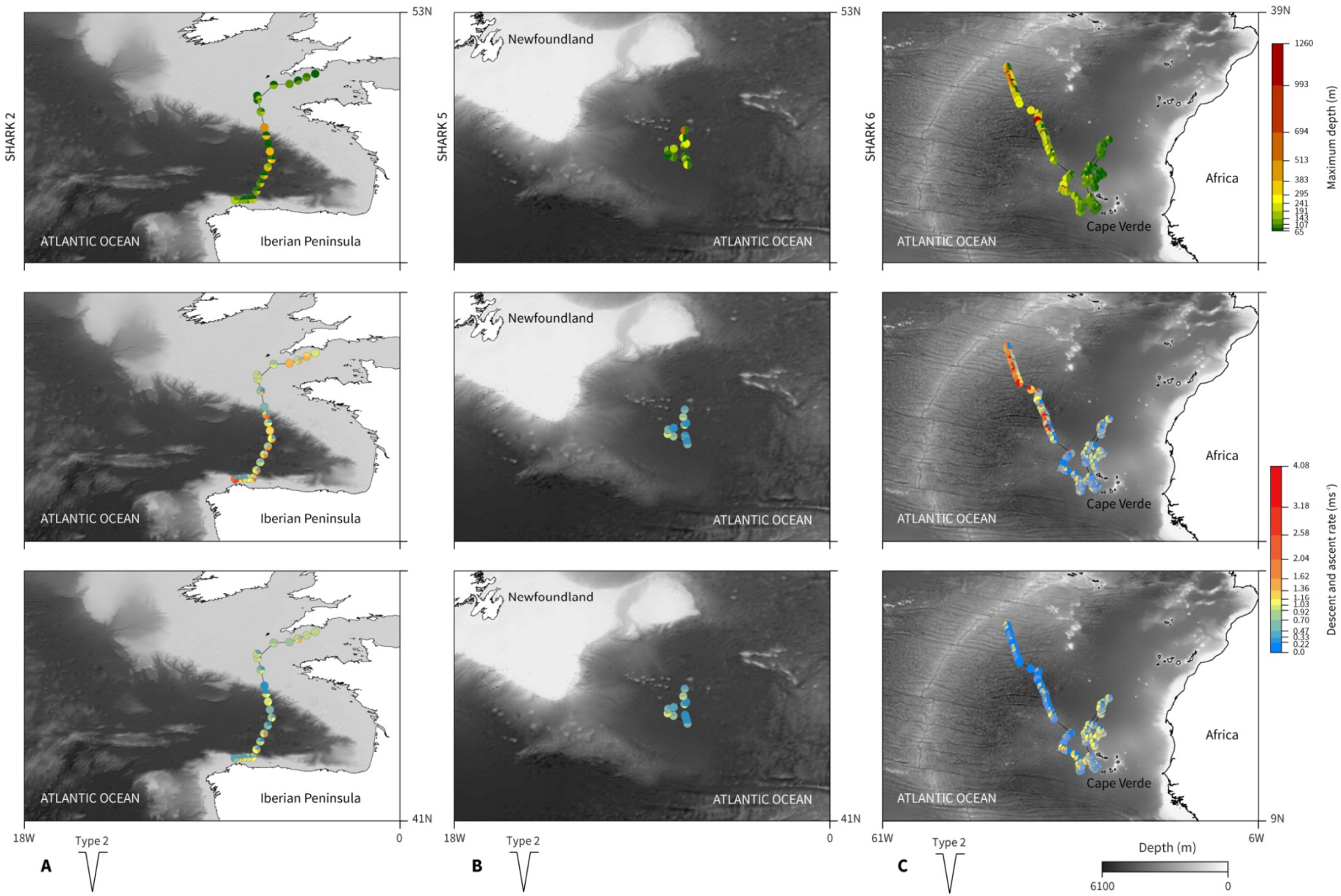

Fig. 9. Summary parameters of Type 2 (V-shaped) dives of three sharks, represented along their horizontal movements. Type 2 dives' maximum depth (top panel), descent rate (middle panel) and ascent rate (bottom panel) of sharks S2 (A), S5 (B) and S6 (C), with pie charts representing the daily proportion of dives within each class of values. Class breaks in color-coded scales were statistically determined, by finding the values' boundaries between which there was a relatively large difference in data value (natural breaks).

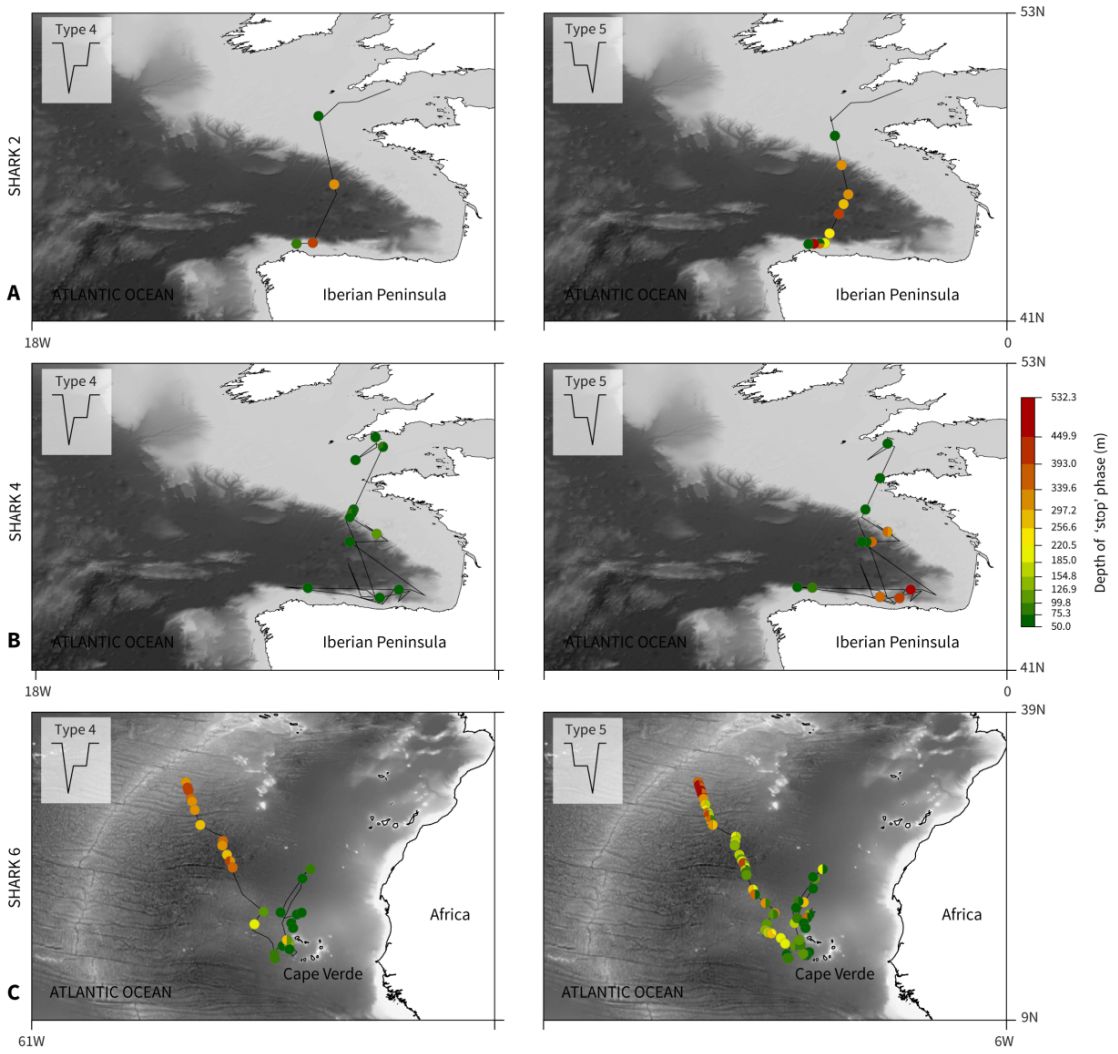

Fig. 10. Summary parameters of Type 4 and 5 dives of three sharks, represented along their horizontal movements. Depth of the 'stop' phase of Type 4 (left panel) and Type 5 (right panel) dives of sharks S2 (A), S4 (B) and S6 (C), with pie charts representing the daily proportion of dives within each class of values. Class breaks in color-coded scales were statistically determined, by finding the values' boundaries between which there was a relatively large difference in data value (natural breaks).

3.3. Diel vertical behaviour

Blue sharks exhibited a very high vertical space use, occupying depths from the surface to a maximum of 1401 m (shark S6). All six individuals presented significant plasticity in their diving behaviour over the time in which they were tracked. Nevertheless, and despite being tagged in different years and in different regions of the North Atlantic Ocean, there were similar patterns in depth distribution over the course of the day among the behavioural sections of different individuals. Essentially, three behavioural modes were detected, which are depicted in Fig. 11.

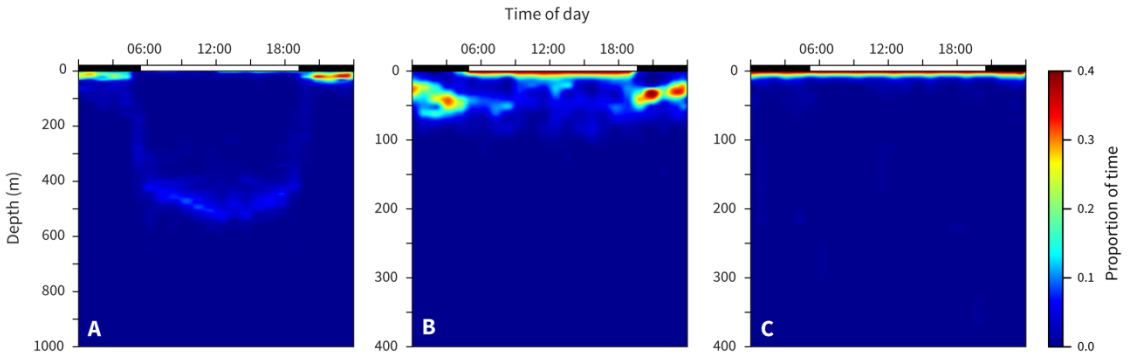

Fig. 11. Normal DVM with permanence at depth (A), reverse DVM (B) and surface-oriented (C) behavioural modes. Mean proportion of time at depth by hour of day of two sharks, S4 (panels A and B, pooled over 22 and 8 days, respectively) and S1 (panel C, pooled over 8 days), depicting the three main behavioural modes exhibited by blue sharks *Prionace glauca* tagged in the North Atlantic Ocean. Black bar indicates night-time and white bar daylight hours, with sunrise and sunset times estimated specifically for each location and time period. Note that the maximum value in the scale bar represents values ≥ 0.4.

Sharks either 1) exhibited normal diel vertical migration (nDVM, Fig. 11A), at shallow depths during the night and spending high proportions of time at deeper waters during the day, 2) performed reverse diel vertical migration (rDVM, Fig. 11B), diving deeper during the night and spending daytime near the surface, or 3) remained in shallow waters throughout both day and night (surface-oriented behaviour, Fig. 11C).

A pattern of nDVM with permanence at depth during daytime was identified in two individuals, shark S4 in productive, off-shelf stratified waters at Bay of Biscay (Fig. 12A) and S6 off western Africa, when the shark was approaching the Western Sahara upwelling front (in this case, the depth of the thermocline changed daily, being about 80 m at the beginning to ca. 50 m near Cape Verde, and including some days in between were water column was frontal). Concerning S4, the depth of the thermocline was also variable between days (usually ~ 50 to 75 m), but the shark remained > 80 % of time above this layer during the night, and spending daytime below it. A second nDVM behaviour, with occupation of both the surface and deeper waters during the day, and surface residence by night, was also detected, mostly on stratified waters off the European shelf (S2, S3 and S4) and off western African shelf (S6, near Cape Verde), but also in an on-shelf tidal induced frontal region near the English Channel (S1, thermocline ~ 25 m; Fig. 12B). In generally well-mixed, isothermal oceanic waters in the western North-Atlantic, shark S5 appeared to exhibit nDVM, nevertheless there were no significant differences between time-weighted average time at depth between day and night in that particular section (Mann-Whitney *U* test with normal approximation, $Z = 1.91$, $p = 0.056$) .

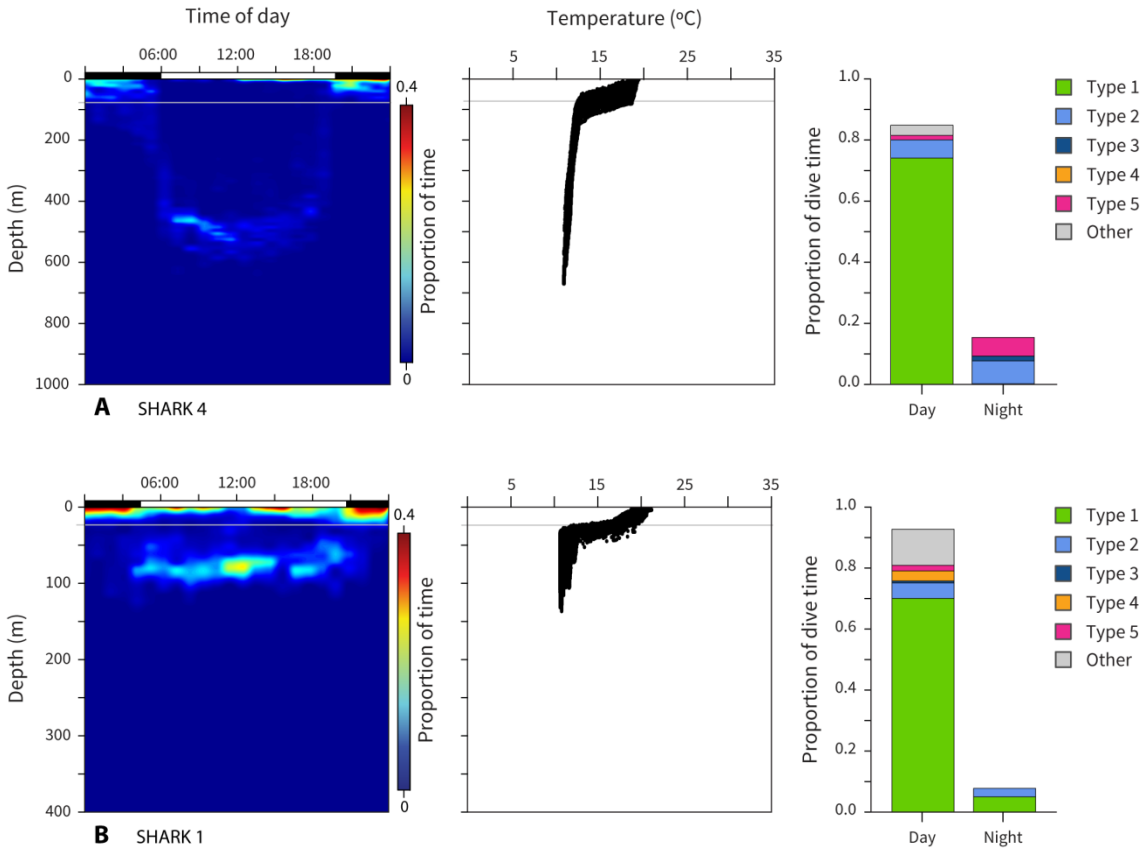

Fig. 12. Normal DVM with permanence at depth (A) and normal DVM (B) behaviour plots from sharks S4 and S1 (both pooled over 9 days), respectively. Left: Mean proportion of time at depth by hour of day (note that the maximum value in the color-coded scale bar represents values ≥ 0.4); black bar indicates night and white bar daylight hours, with sunrise and sunset times estimated specifically for the time period of this behavioural section; horizontal grey line represents thermocline depth. Centre: temperature-at-depth profile (depth scale similar to left panel; thermocline depth represented by horizontal grey line). Right: proportional occurrence of dive classes by day and night (relative to total dive time).

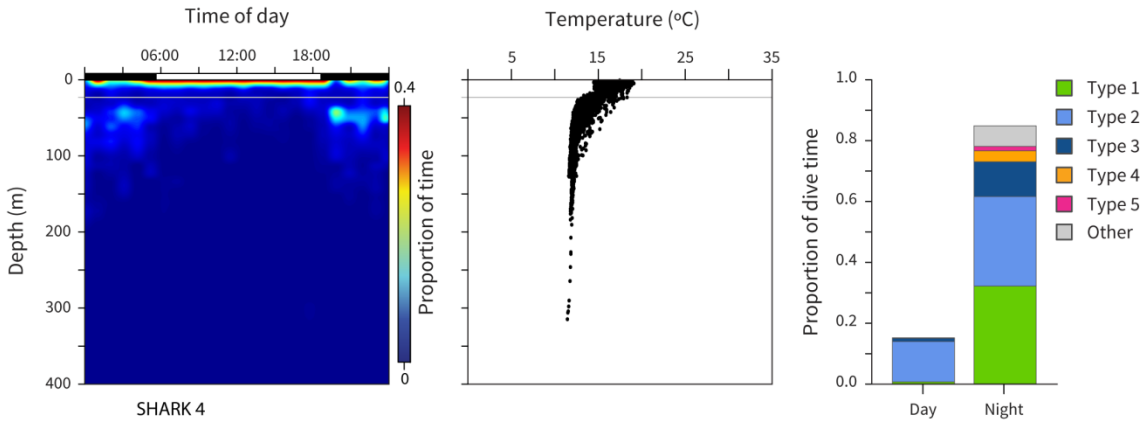

Fig. 13. Reverse DVM behaviour plot from shark S4 (pooled over 7 days). Left: Mean proportion of time at depth by hour of day (note that the maximum value in the color-coded scale bar represents values ≥ 0.4); black bar indicates night and white bar daylight hours, with sunrise and sunset times estimated specifically for the time period of this behavioural section; horizontal grey line represents thermocline depth. Centre: temperature-at-depth profile (depth scale similar to left panel; thermocline depth represented by horizontal grey line). Right: proportional occurrence of dive classes by day and night (relative to total dive time).

Reverse DVM was observed in one shark (S4, tagged in 2007 at the Bay of Biscay) when diving in on-shelf waters and also near shelf-edge frontal waters (e.g. Fig. 13). In both these sections, the depth of the thermocline was variable, fluctuating from ~ 20 to 30 m and interspersed with some days where the water column appeared generally well-mixed.

Surface-oriented behavioural mode was displayed by the two sharks tagged in 2006 (S1 and S2) and also by shark S3 tagged in 2007, in stratified waters in and off the European shelf (Fig. 14A) and also near the shelf-edge, around tidal induced frontal features. S3 depth occupation presented a few excursions below the thermocline, which was highly variable between each days, but never below the deepest thermocline detected (~ 100 m). The two sharks tagged in oceanic waters (S5 and S6) also exhibited an irregular diving pattern, with no diel periodicity and diving depth ranges of 600 m to > 1000 m, associated with stratified deep-oceanic waters (Fig. 14B).

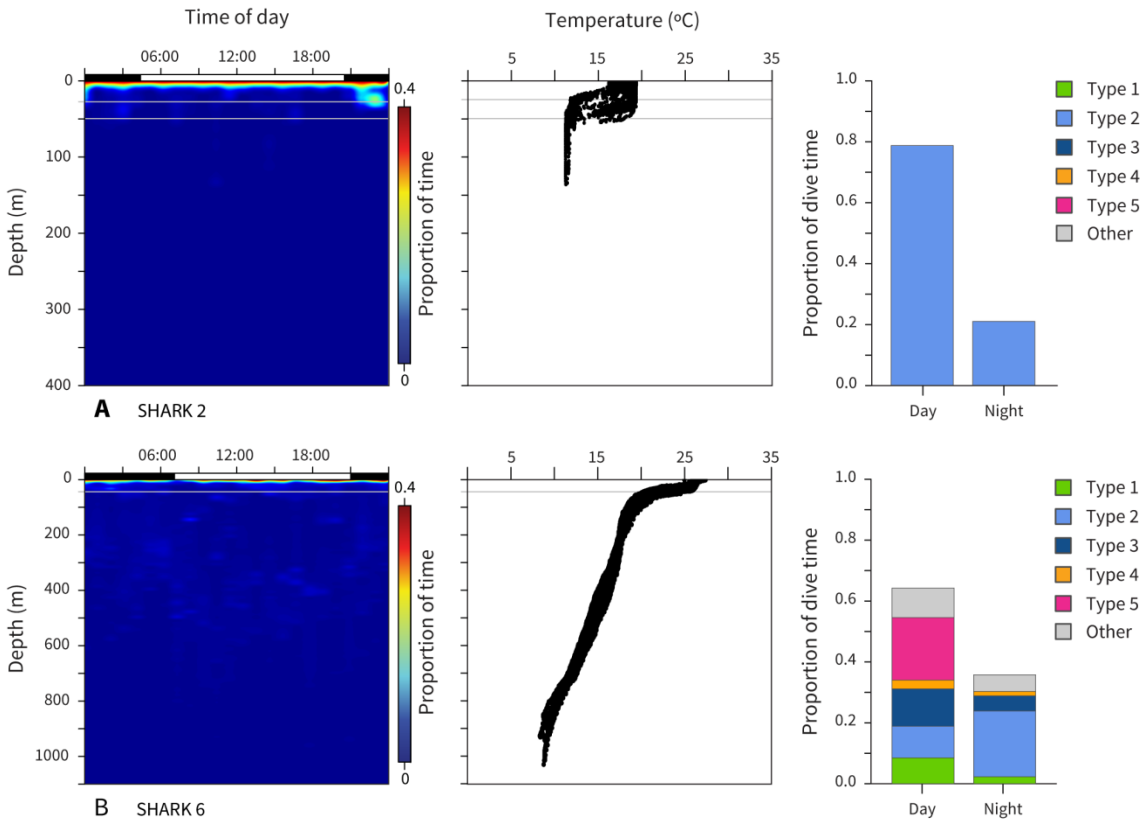

Fig. 14. Surface-oriented (A) and irregular (B) behaviour plots from sharks S2 (pooled over 4 days) and S6 (pooled over 7 days), respectively. Left: Mean proportion of time at depth by hour of day (note that the maximum value in the color-coded scale bar represents values ≥ 0.4); black bar indicates night and white bar daylight hours, with sunrise and sunset times estimated specifically for the time period of this behavioural section; horizontal grey line represents thermocline depth. Centre: temperature-at-depth profile (depth scale similar to left panel; thermocline depth represented by horizontal grey line). Right: proportional occurrence of dive classes by day and night (relative to total dive time). Note the highly variable water column stratification in A (central panel).

3.3.1. Dive shape analysis – day *vs.* night dives

In view of the marked variability in diel behaviour, with strong patterns of normal and reverse diel vertical migration being displayed by several individuals, the analysis of blue sharks' dive shape further considered a division of dives by day- and night-time. As expected, this approach yielded insightful results, not only in respect to the characterization of dive classes between the two groups (Table 5 and Fig. 15), but also when comparing them in association with 'behavioural modes' and water column thermal profiles.

On average, Type 1 (U-shaped) and Type 5 (right-V shaped) dives were predominantly performed by day (19.2 % and 2.3 % against 7.1 % and 0.8 % by night, respectively), with daytime Type 1 dives comprising a very large proportion of total diving time (53.3 %). On the other hand, Type 2 (V-shaped) dives were most frequently displayed by night (18.1 % by day and 24.1 % by night). The remaining classes, Types 3, 4 and 5 (W-, left-V and right-V shaped), showed similar frequencies by day and night, but night-time Type 4 and Type 5 dives were usually shorter in duration (Fig. 15A). Some general characteristics of the identified dive types performed by day and night are illustrated in Fig. 15 B-E and in Table 5. Considering Type 1 dives alone, significant differences between mean bottom phase duration and also mean dive depth were detected when comparing day and night dives (Mann-Whitney U-tests with normal approximation: mean daytime bottom duration = 96.37 min, mean night-time bottom duration = 19.35 min, $Z = 18.52$, $p < 0.001$; mean daytime depth = 228.67 m, mean night-time depth = 110.72 m, $Z = 14.46$, $p < 0.001$). Dives performed during the day presented a much larger range of bottom phase duration, up to almost 17 h (Fig. 15B). V-shaped dives, Type 2, also exhibited significant differences between daytime/night-time dives concerning mean dive duration, but not in respect to mean maximum depth (Mann-Whitney U-tests with normal approximation: mean daytime dive duration = 15.84 min, mean night-time dive duration = 11.92 min, $Z = -3.13$, $p = 0.002$; mean daytime maximum depth = 139.33 m, mean night-time maximum depth = 105.75 m, $Z = 1.62$, $p = 0.104$) (Fig. 15C). When comparing the ratio of descent/ascent speeds between Type 2 dives performed by day and night, significant differences were detected between the means of the two groups (t-test for unequal variances: mean daytime ratio = 1.66, mean night-time ratio= 2.03, $t(1518) = -2.26$, $p = 0.024$) (Fig. 15D). Additionally, when considering epipelagic (0 – 200 m) and mesopelagic (> 200 m) dives as separate groups within day- and night-time dives, significant differences were also observed (t-test for unequal variances: Day, epipelagic mean ratio = 1.33, mesopelagic mean ratio = 3.51, $t(384) = -9.28$, $p < 0.001$; Night,

epipelagic mean ratio = 1.41, mesopelagic mean ratio = 6.80, t (1132) = - 22.82, p < 0.001), with mesopelagic dives presenting a more flattened and left-skewed distribution on both day and night groups (Fig. 15E). When taking a closer look at dive classes on each individual separately, some similarities in the frequency and proportion of time performing each type of dive were detected among the six blue sharks, with regard to behavioural sections with the same diel pattern of diving behaviour (nDVM, rDVM, surface-oriented). Sections where sharks exhibited nDVM, in regions with stratified waters, were usually characterized by having days with several Type 1 dives (U-shaped), that comprised a very large proportion of diving time, and nights with very few dives, typically V-shaped (Type 2). In the Bay of Biscay, S1 exhibited a few Type 2 and 'Other' dives by day as well, and S2 mostly Types 2, 3 and 5 when off the European shelf and Types 1 and 5 (and a few Type 4) at the shelf-edge off northern Spain. When sharks were undertaking rDVM, they mostly performed Type 2 and 'Other' dives both during day and night-time, and also a few Type 1 when diving in on-shelf isothermal waters and almost exclusively Types 1 to 3 at night in shelf-edge frontal waters. Surface-oriented behaviours were variable, with S1 displaying Types 1, 3 and 4 mainly by day at stratified shelf-break waters and Type 1 and 2 dives both at day and night when diving off-shelf. S6 irregular behaviour comprised several Type 5 dives by day and frequent Type 2 dives by night, whereas S5 presented a few Type 1 dives by day, and short Type 1, 2 and 3 dives by night.

Table 5. Day- and night-time proportional occurrence (by frequency and by total dive time) and general descriptive statistics of the five dive classes (Types 1 to 5) performed by blue sharks, *Prionace glauca*. Results are presented as mean with 1 SD in parenthesis.

Dive class	**Type 1**		**Type 2**		**Type 3**		**Type 4**		**Type 5**	
	Day	*Night*	*Day*	*Night*	*Day*	*Night*	*Day*	*Night*	*Day*	*Night*
Frequency	0.19 (0.14)	0.07 (0.05)	0.18 (0.13)	0.24 (0.13)	0.02 (0.01)	0.02 (0.02)	0.02 (0.01)	0.01 (0.004)	0.02 (0.03)	0.01 (0.01)
Proportion of dive time	0.53 (0.18)	0.06 (0.04)	0.06 (0.04)	0.07 (0.03)	0.03 (0.03)	0.02 (0.03)	0.03 (0.03)	0.01 (0.004)	0.07 (0.13)	0.01 (0.01)
Mean dive duration (min)	170.65 (123.08)	35.03 (18.43)	14.36 (5.08)	11.98 (3.54)	59.19 (27.71)	40.22 (24.10)	63.98 (45.83)	31.82 (22.76)	79.30 (59.28)	45.06 (25.47)
Mean maximum dive depth (m)	322.71 (178.37)	105.15 (37.36)	127.72 (47.18)	98.11 (16.61)	325.62 (202.25)	125.78 (31.40)	298.87 (204.44)	129.86 (63.53)	342.60 (249.80)	144.79 (54.37)

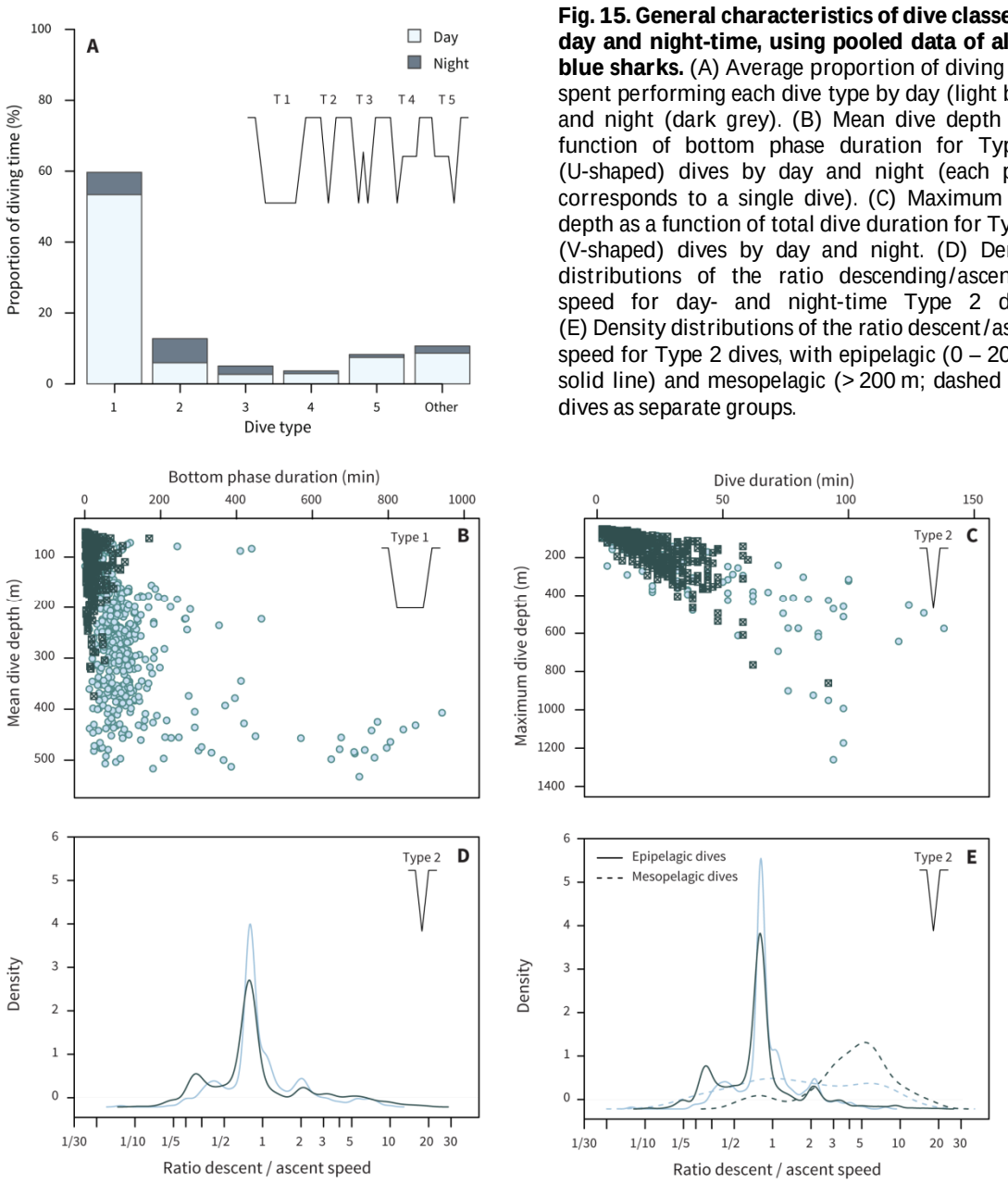

Fig. 15. General characteristics of dive classes by day and night-time, using pooled data of all six blue sharks. (A) Average proportion of diving time spent performing each dive type by day (light blue) and night (dark grey). (B) Mean dive depth as a function of bottom phase duration for Type 1 (U-shaped) dives by day and night (each point corresponds to a single dive). (C) Maximum dive depth as a function of total dive duration for Type 2 (V-shaped) dives by day and night. (D) Density distributions of the ratio descending/ascending speed for day- and night-time Type 2 dives. (E) Density distributions of the ratio descent/ascent speed for Type 2 dives, with epipelagic (0 – 200 m; solid line) and mesopelagic (> 200 m; dashed line) dives as separate groups.

3.4. First results on the dive shape analysis of a planktivorous shark species, *Cetorhinus maximus*

Depth time series records at fine temporal resolution were successfully obtained for six basking sharks tagged in the eastern North Atlantic Ocean. Only two were sexed with certainty: two females of 4.5 and 6 m total length (TL); the remaining ranged in length from 2.5 to 6.5 m TL.

The basking sharks' time series of vertical diving movements also comprised different patterns of vertical space use that were objectively partitioned using a Split-Moving Window analysis. In general, all individuals performed continuous vertical movements through the water column, occupying depths ranging from the surface to nearly 200 m. On the other hand, very extensive depth excursions lasting more than one day, and up to a maximum of approximately 10 days, were also observed in some individuals.

A total of 7207 dives were identified for basking sharks, with sharks exhibiting a mean of 22.85 ± 11.50 dives per day (range: 12.92 – 37.19). Nevertheless, only 5928 of these dives were considered for subsequent dive shape analyses due to limitations in delineating dive phases when considering the full resolution of the archival data set (see 'Methods' section for clarification). Approximately 6.7% of the total number of dives still presented misidentified phases, and for these cases a manual assignment of phases was performed (see 'Methods'). Manual dive classification categorized dives into the same five general types identified for blue sharks, plus four additional sub-types only detected on this species. The mean proportion of each dive class, by frequency and also relative to the total diving time, is presented in Table 6 and Table 7 and in Fig. 16. Type 1 (U-shaped) and Type 2 (V-shaped) dives were the most frequently performed in total, similarly to the blue sharks, and again with Type 2 dives comprising ca. 50% of dives by frequency but a very short slice of total dive time (10.3 %), while Type 1 dives represented 24.1 % of the total number of dives and 58.5 % of total dive time (Table 6). Types 3, 4 and 5 and also 1A to 1D represented less than 5 % of the total number of basking sharks' dives and of total dive time, except for Type 1C dives (irregular U-shaped; 14.6 % of total dive time) (Table 6 and Table 7). Shark S8 performed several Type 1C dives that comprised a substantial proportion of its total dive time (78.6 %). Dives that did not fit any of these classes comprised 15.3 % of dives by frequency, corresponding to about 5.6 % of basking sharks' dive time.

Table 6. Proportional occurrence (by frequency and by total dive time) and general descriptive statistics of the main five dive classes (Types 1 to 5) performed by basking sharks, *Cetorhinus maximus*. Results are presented as mean with 1 SD in parenthesis. Dives that did not fit any of these general types were assigned to class 'Other'.

Dive class	Type 1	Type 2	Type 3	Type 4	Type 5	Other
Frequency	0.24 (0.04)	0.49 (0.04)	0.04 (0.02)	0.03 (0.01)	0.03 (0.02)	0.15 (0.05)
Proportion of dive time	0.58 (0.25)	0.10 (0.08)	0.03 (0.02)	0.03 (0.03)	0.02 (0.01)	0.06 (0.05)
Mean dive duration (min)	178.72 (150.61)	9.37 (3.68)	34.66 (19.83)	37.65 (17.18)	35.97 (20.46)	-
Mean maximum dive depth (m)	62.75 (17.62)	41.79 (9.18)	56.13 (14.57)	52.98 (15.16)	56.32 (21.78)	-

Table 7. Proportional occurrence (by frequency and by total dive time) and general descriptive statistics of the additional dive classes (Types 1A to 1D) only occurring on basking sharks (presented as mean with 1 SD in parenthesis).

Dive class	Type 1A	Type 1B	Type 1C	Type 1D
Frequency	0.001 (0.002)	0.001 (0.002)	0.01 (0.03)	0.004 (0.01)
Proportion of dive time	0.01 (0.02)	0.007 (0.01)	0.15 (0.31)	0.02 (0.04)
Mean dive duration (h)	10.67 (2.40)	9.56 (6.38)	21.09 (20.66)	18.96 (15.80)
Mean maximum dive depth (m)	126.17 (40.55)	129.33 (39.63)	144.12 (41.19)	139.63 (46.56)

The observed probabilities of changing from one dive type at a given time t to another at time (t + 1) were more persistent among basking sharks' individuals (Table 8). Similarly to blue sharks, if a basking shark was performing a Type 1 dive (U-shaped), it would most likely continue performing the same type and if it changed it would probably be to a Type 2 (V-shaped) dive. A basking shark performing a Type 2 dive is expected to remain displaying this class, and in case it changes it is probably to a Type 1 dive. Types 3, 4 and 5 were almost certainly followed by Type 2 dives, or eventually by Type 1 or irregular (unclassified) dives, again in accordance with blue sharks. Concerning Type 1A dives, when a basking shark was performing this class of dives it would probably change to a Type 1 dive, or to an irregular (unclassified) dive. Type 1B dives were almost always followed by Type 2 dives or in lesser chance by Type 1/Type 1B. The probabilities of changing from Type 1C dives to another class did not show much consistency among individuals, with a shark remaining performing the same class almost every time, but

other individuals changing to Type 1, Type 2 or even Type 5 and irregular (unclassified) dives. When basking sharks were exhibiting Type 1D dives it was most probable that they performed a Type 1 dive next, or changed to an irregular or Type 2 dive. Once again similarly to blue sharks, in all basking sharks the irregular dives grouped in the class 'Other' were usually performed in series, and if a change occurred it was most likely to a Type 2 or to a Type 1 dive.

Table 8. Transition matrix averaged for the six basking sharks, showing the mean probabilities of changing from one dive type at a given time *t* to another at time (*t* + 1).

Dive class	Type 1 (t + 1)	Type 2 (t + 1)	Type 3 (t + 1)	Type 4 (t + 1)	Type 5 (t + 1)	Type 1A (t + 1)	Type 1B (t + 1)	Type 1C (t + 1)	Type 1D (t + 1)	Other (t + 1)
Type 1 (t)	0.45	0.36	0.04	0.03	0.02	0.001	0.003	0.01	0.01	0.08
	(0.05)	(0.04)	(0.02)	(0.03)	(0.02)	(0.002)	(0.01)	(0.01)	(0.01)	(0.04)
Type 2 (t)	0.17	0.63	0.04	0.02	0.02	0.002	0.002	0.01	0.004	0.10
	(0.04)	(0.04)	(0.02)	(0.01)	(0.01)	(0.002)	(0.002)	(0.01)	(0.005)	(0.05)
Type 3 (t)	0.23	0.49	0.08	0.05	0.03	0.01	0.00	0.01	0.01	0.10
	(0.11)	(0.13)	(0.05)	(0.04)	(0.02)	(0.02)	(0.00)	(0.01)	(0.02)	(0.04)
Type 4 (t)	0.16	0.42	0.06	0.08	0.04	0.00	0.01	0.00	0.00	0.24
	(0.08)	(0.17)	(0.11)	(0.05)	(0.03)	(0.00)	(0.01)	(0.00)	(0.00)	(0.10)
Type 5 (t)	0.22	0.46	0.05	0.02	0.08	0.00	0.00	0.01	0.05	0.13
	(0.08)	(0.12)	(0.09)	(0.04)	(0.05)	(0.00)	(0.00)	(0.01)	(0.06)	(0.09)
Type 1A (t)	0.42	0.00	0.17	0.00	0.08	0.00	0.00	0.00	0.00	0.33
	(0.14)	(0.00)	(0.29)	(0.00)	(0.14)	(0.00)	(0.00)	(0.00)	(0.00)	(0.29)
Type 1B (t)	0.17	0.67	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00
	(0.29)	(0.29)	(0.00)	(0.00)	(0.00)	(0.00)	(0.29)	(0.00)	(0.00)	(0.00)
Type 1C (t)	0.28	0.30	0.01	0.00	0.13	0.00	0.004	0.18	0.004	0.10
	(0.26)	(0.23)	(0.01)	(0.00)	(0.25)	(0.00)	(0.01)	(0.36)	(0.01)	(0.19)
Type 1D (t)	0.61	0.11	0.04	0.00	0.04	0.00	0.00	0.00	0.04	0.17
	(0.35)	(0.19)	(0.06)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.06)	(0.29)
Other (t)	0.17	0.31	0.03	0.03	0.05	0.004	0.00	0.001	0.00	0.41
	(0.04)	(0.02)	(0.02)	(0.02)	(0.06)	(0.00)	(0.00)	(0.002)	(0.00)	(0.08)

3.4.1. General characterization of dive types

Some characteristics of the dive types identified for basking sharks are illustrated in Fig. 16B-E and in Table 6 and Table 7. Type 1 dives, in parallel with blue sharks, exhibited a very large range of dive duration, with a few dives extending far more than 24 h. In basking sharks, this class of dives reached a wide array of depths, from the top 10 m to almost 200 m. Types 2 to 5 presented a similar depth range, however with durations usually below 2 h. Concerning the additional classes displayed by basking sharks, Types 1A, 1B and 1D were very irregular, mostly presenting total durations of less than a day and with maximum depths ranging from ca. 70 to 180 m. Type 1C dives generally occurred below 120 m and extended for several hours or even days (Fig. 16B). Basking sharks presented very low descent and ascent rates, usually below 0.5 ms-1 and to a maximum of 2.5 ms-1 (Fig. 16C, D), about half of blue sharks' speed range (Fig. 6C, D). Again, a significant positive correlation between the depth of the stop in ascent or descent, respectively, and the maximum depth of the dive was detected in Type 4 and Type 5 dives (Fig. 16E; Type 4 dives: Spearman's rank correlation coefficient $\rho = 0.68$, $p < 0.001$; Type 5: Spearman's rank correlation coefficient $\rho = 0.55$, $p < 0.001$).

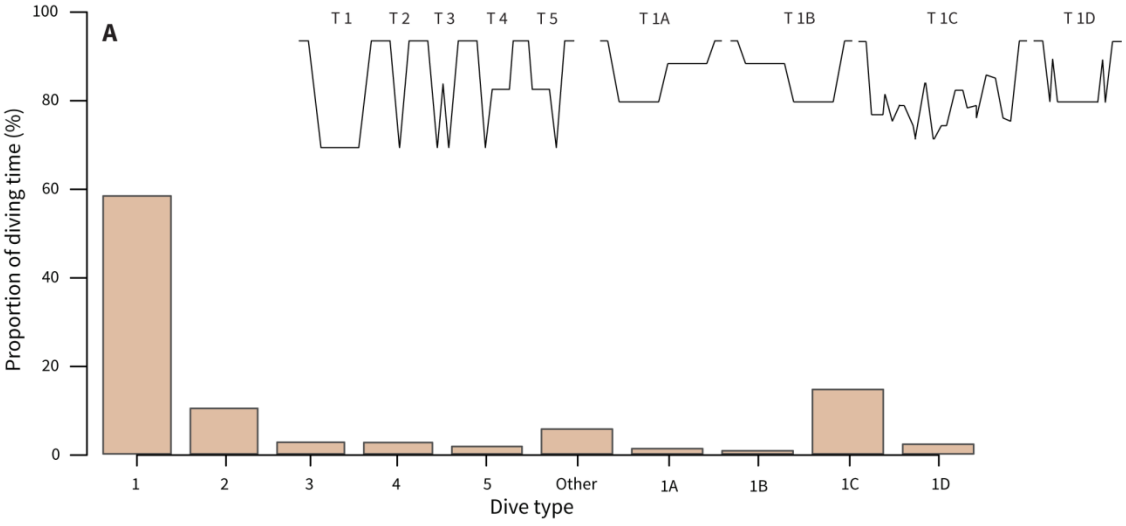

Fig. 16. General characteristics of dive classes, using pooled data of all six basking sharks. (A) Average proportion of diving time spent performing each dive type. (continued)

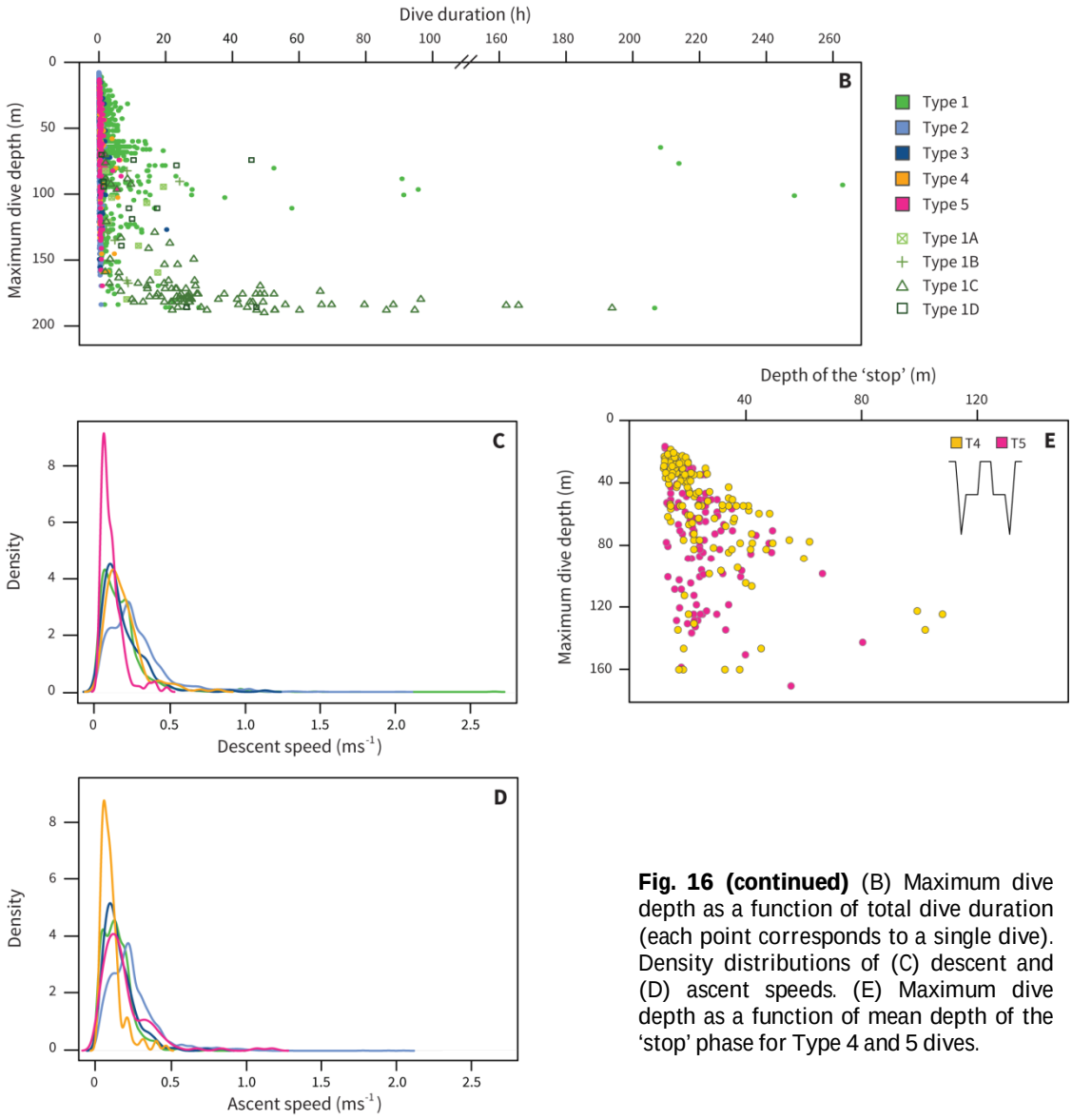

Fig. 16 (continued) (B) Maximum dive depth as a function of total dive duration (each point corresponds to a single dive). Density distributions of (C) descent and (D) ascent speeds. (E) Maximum dive depth as a function of mean depth of the 'stop' phase for Type 4 and 5 dives.

3.4.2. Diel vertical behaviour

Similarities in depth distribution over the course of the day among behavioural sections of different individuals were observed as well, and in general equivalent to those detected on blue sharks. The three main behavioural 'modes' identified on blue sharks, normal and reverse diel vertical migration and surface-oriented behaviour, were also detected for basking sharks (Fig. 17), plus irregular diving behaviour with no apparent diel variation. An additional depth distribution behaviour was observed in one basking shark, which was characterized by continuous permanence at depth during several days. Such behavioural patterns comprised almost exclusively U-shaped dives (Type 1) during both day and night (Fig. 18).

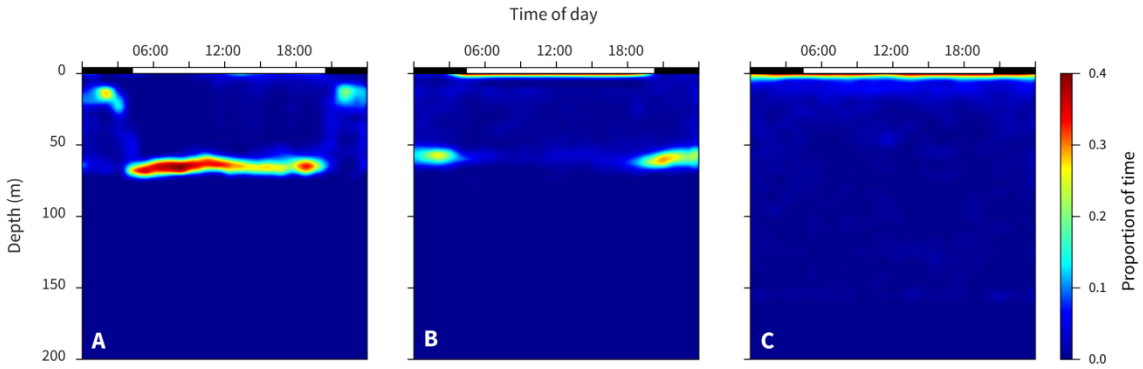

Fig. 17. Normal DVM with permanence at depth (A), reverse DVM (B) and surface-oriented (C) behavioural modes. Mean proportion of time at depth by hour of day of three sharks, S12 (panel A, pooled over 18 days), S8 (panel B, pooled over 36 days) and S7 (panel C, pooled over 18 days), depicting the three main behavioural modes exhibited by basking sharks *Cetorhinus maximus* tagged in the North Atlantic Ocean. Black bar indicates night-time and white bar daylight hours, with sunrise and sunset times estimated specifically for each location and time period. Note that the maximum value in the scale bar represents values ≥ 0.4.

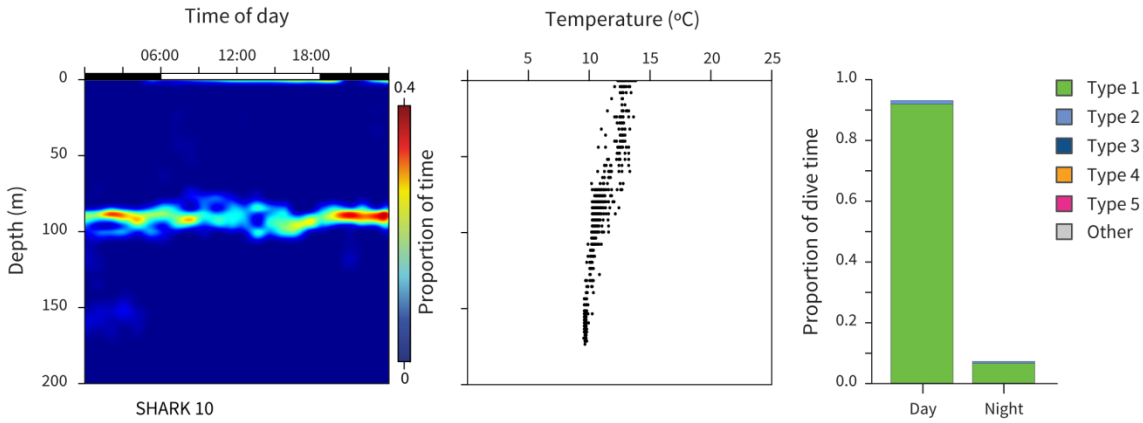

Fig. 18. Permanence at depth behaviour plot from shark S10 (pooled over 4 days). Left: Mean proportion of time at depth by hour of day (note that the maximum value in the color-coded scale bar represents values ≥ 0.4); black bar indicates night and white bar daylight hours, with sunrise and sunset times estimated specifically for the time period of this behavioural section). Centre: temperature-at-depth profile (depth scale similar to left panel). Right: proportional occurrence of the main dive classes by day and night (relative to total dive time).

3.4.3. Dive shape analysis – day *vs.* night dives

Regarding diel differences in the observed dive classes, only the five main types also identified for blue sharks were considered, both because Types 1A to 1D usually extended for several days, therefore classifying them as day or night-time dives hardly makes sense, and also since the main goal of this analysis is to compare the characteristics of dive types on both species of sharks.

In basking sharks, Type 1 dives also comprised a higher proportion of diving time by day than by night (34.3 % by day and 24.2 by night; Fig. 19), even though with proportions

not as disparate as those of blue sharks (53.3 % against 18.5 %). Unlike blue sharks, basking sharks also performed Type 2 dives more frequently by day. The remaining classes presented very low frequencies in both periods. Considering Type 1 dives alone, small but significant differences between mean bottom phase duration and also mean dive depth were detected when comparing day and night-time dives (Mann-Whitney U-tests with normal approximation: mean daytime bottom duration = 158.67 min, mean night-time bottom duration = 163.03 min, $Z = -4.33$, $p < 0.0001$; mean daytime depth = 61.58 m, mean night-time depth = 49.25 m, $Z = 8.16$, $p < 0.0001$). V-shaped dives, Type 2, also exhibited significant differences between daytime/night-time dives concerning mean dive duration and mean maximum depth (Mann-Whitney U-tests with normal approximation: mean daytime dive duration = 8.96 min, mean night-time dive duration = 11.32 min, $Z = -5.62$, $p < 0.0001$; mean daytime maximum depth = 44.67 m, mean night-time maximum depth = 39.17 m, $Z = 4.32$, $p < 0.0001$). When comparing the ratio of descent/ascent speeds in Type 2 dives performed by day and night, the majority of dives in both groups presents a ratio close to one, that is, similar descent and ascent rates. Significant differences were detected between the means of the two groups (t-test for unequal variances: mean daytime ratio = 1.32, mean night-time ratio = 1.16, $t(2955) = -5.6$, $p < 0.0001$).

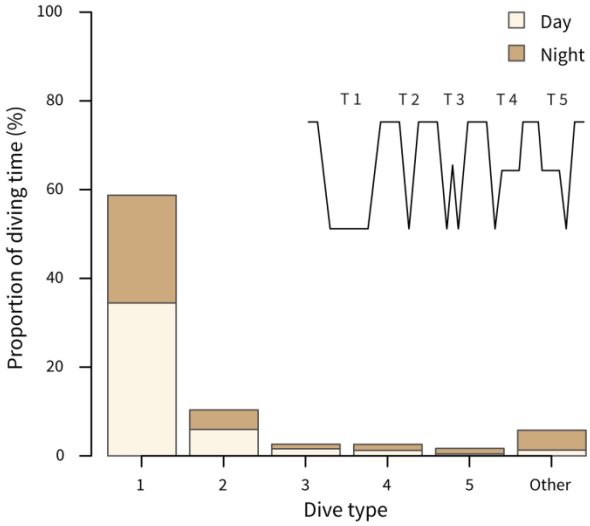

Fig. 19. Five main dive classes by day and night-time, using pooled data of all six basking sharks. Average proportion of diving time spent performing each dive type by day (light brown) and night (dark brown).

4. DISCUSSION

In this study, archival data retrieved from blue sharks tagged with satellite-linked archival transmitters suggests that in the North Atlantic blue sharks shift their vertical movements and diving behaviour according to changing oceanographic conditions. Blue sharks exhibited predominantly Type 1 dives (U-shaped) in high productivity regions, either stratified waters or areas near thermal fronts, whereas the remaining classes of dives, namely Type 2 (V-shaped), were usually displayed over more oligotrophic waters. This species presented a very high vertical space use, with the deepest record of 1401 m, and three frequent diel patterns common across different individuals tagged in diverse areas of the North Atlantic Ocean.

4.1. Dive shape analysis

Previous studies have investigated the horizontal and vertical spatial dynamics of pelagic predators in the North Atlantic and have observed that, overall, they extensively use several habitats over different times of the year (e.g. Hays, Houghton, & Myers 2004, Block et al. 2005, Gore et al. 2008, Queiroz et al. 2010), and in some cases display site-fidelity to particular areas (e.g. Walli et al. 2009, Queiroz et al. 2012). How the animals utilize these distinct regions has recently been examined using high-resolution dive profiles obtained from archival tags. Dives were clustered into several categories based on their two-dimensional shape (i.e., depth versus time), and it is hypothesized that each class of dives, along with their frequency, persistence and characteristics, may be related to distinct activities such as foraging or travelling (Horodysky et al. 2007, Thomson et al.

2011, Dragon et al. 2012). Here, five dive types have been identified for the six blue sharks tagged in the North Atlantic in four different years (2006, 2007, 2010 and 2011). These dive types, and also some dive parameters considered biologically more relevant for each type, were spatially represented along the sharks' estimated geolocations. Seasonal composite representations of sea surface temperature and chlorophyll *a* concentration (used as a proxy for prey densities) were also obtained in order to complement habitat use assessment based on the shape of blue sharks' dives.

Several hypotheses have been advanced to account for commonly observed patterns in diving behaviour of blue sharks, namely foraging, thermoregulation, predator avoidance and navigational processes (e.g. Carey & Scharold 1990, Campana et al. 2011), and that may also be linked to particular functions of these dive types. Navigation has never been empirically tested as a factor influencing the behaviour of sharks. Predator avoidance has also been discarded as a likely explanation since the blue sharks tagged in the North Atlantic by Queiroz et al. (2012), both juveniles, sub-adults and adults (and some of which were included in this study), did not exhibit differences in diel behaviour according to life stage. Such differences were expected if anti-predator behaviour was causing the observed variability. These authors also discarded behavioural thermoregulation since no correlation between vertical movements and thermocline depths was detected. Considering as well the fact that the identified dive shapes and overall patterns of diving behaviour observed in this study occurred across all individuals, tagged in different years and in three different regions of the North Atlantic Ocean, they probably represent foraging behaviours. Each dive type may therefore account for activities such as searching for prey or feeding behaviours, as proposed in other studies on different pelagic species (Baechler et al. 2002, Horodysky et al. 2007, Wilson & Block 2009). In this study, Type 1 (U-shaped) dives comprised a very high proportion of total diving time in all blue sharks (> 50 % on all but shark S2) and were generally performed consecutively over the day, and sometimes during several days. This type of dives presented a bottom phase of large duration when compared to the remaining types, sometimes extending to more than 6 h, and these very extensive dives were also typically performed within a uniform depth layer. In three of the sharks the higher values of vertical sinuosity of the bottom phase in Type 1 dives were observed in the regions where this class of dives was predominant (with the remaining sharks presenting low sinuosity values over the entire track). High sinuosity, resulting from multiple 'wiggles' in the bottom phase, has been suggested to be related to foraging in air-breathing divers such as sea lions, southern elephant seals and wandering albatrosses (Weimerskirch et al. 2007, Villegas-Amtmann et al. 2008, Dragon et al. 2012). In optimal foraging theories, the time a

forager spends in a specific area is assumed to be related to its prey richness (Stephens & Krebs 1986, Mori et al. 2005, Austin et al. 2006). In fact, studies in the planktonic basking shark conducted near the European shelf, off England, have observed that the sharks' behaviour was related to the abundance and distribution of prey. Basking sharks spent progressively more time in regions with high densities of large zooplankton species (Sims & Quayle 1998). Furthermore, the time spent swimming at the surface was also found to increase significantly with increasing minimum zooplankton densities (Sims, Southall, Merrett, et al. 2003). This species was also observed to select vertical habitat based on the vertical migrations of its prey species (Sims et al. 2005). The basking sharks for which archival data was analysed in this study remained near thermally stratified water masses and thermal fronts off England during the tracking period (Sims, Southall, Richardson, et al. 2003, Sims et al. 2005). In this study, Type 1 dives were predominant when considering the total time basking sharks spent diving, and could extend over several hours and even days. These Type 1 dives were also generally performed at relatively uniform depths. Additionally, four new dive types were observed in basking sharks in this study, which were broadly U-shaped but with slight variations in the bottom phase (Types 1A to 1D). These supplementary types presented very long durations and general permanence at depth as well. Thus, considering the known selective behaviour of basking sharks at small spatial scales, it is probable that these dives represent foraging on aggregated zooplankton prey patches. Since blue sharks' Type 1 dives were also characterized by a bottom phase of prolonged duration at a relatively constant depth, such dive types may likewise correspond to foraging behaviour. In air-breathing marine vertebrates, on which most studies of dive shape analysis have been undertaken (and usually with additional information regarding feeding indices), there is in fact substantial evidence that U-shaped dives correspond to feeding events, for example based on positive correlations between food intake and high duration of the bottom phase (Lesage et al. 1999, Baechler et al. 2002). Similar Type 1 (U-shaped) dives (confined to a certain depth for extended periods of time) have also been observed in white marlins, *Tetrapturus albidus* (Horodysky et al. 2007). Additionally, Wilson and Block (2009), even though not classifying each dive independently but the general shape of the dive profile, have observed a prevalence of U-shaped profiles in four hotspots that correspond to known Atlantic bluefin tuna (*Thunnus thynnus*) feeding areas. Both these studies contribute to the assumption that Type 1 dives (U-shaped) represent foraging dives in pelagic predators. In this study, blue sharks' Type 1 dives were generally performed in series over each day, in some cases being the prevalent type over several days. These aggregations of Type 1 dives were usually displayed in regions with higher chlorophyll *a* concentration, hence more productive waters, generally

near frontal features or upwelling areas. Additionally, in three of the sharks the vertical sinuosity of the bottom phase in this class of dives was greater towards more productive waters. These findings strengthen the hypothesis that Type 1 dives (U-shaped) represent foraging behaviours, probably on aggregated prey patches. Type 2 dives (V-shaped) were the most frequently performed by blue sharks in this study. These dives presented short durations and a wide range of maximum depth (up to nearly 1400 m in one of the sharks). Type 2 dives were observed to be commonly displayed in consecutive series, but in some cases also interspersed among other types. It is hypothesized that by swimming up and down through the water column and crossing between different depth layers, foragers may increase the probability of detecting olfactory cues, since odour trails essentially propagate in the ocean at a horizontal plane owing to current shear between different density layers (Carey & Scharold 1990, Pade et al. 2009). V-shaped dives have been observed in several species of marine predators and are thought to correspond to transiting behaviour (Horodysky et al. 2007, Wilson & Block 2009). In theory, an animal transiting through a certain area (and not feeding) is expected to swim minimizing its cost of locomotion (Iosilevskii et al. 2012). Recent studies investigating optimality in movement strategies and dive geometry of fish and marine mammals have suggested that V-dives may allow such optimality, coupling large horizontal displacements to low energy expenditure (e.g. Gleiss et al. 2011). This is achieved by swimming at slow speeds during the descent, taking advantage of buoyancy to glide, and ascending with higher locomotory activity (Williams et al. 2000, Gleiss et al. 2011, Iosilevskii et al. 2012). Additionally, these dives may also allow the individuals to scan the water column for opportunistic prey encounters or olfactory cues. Bluefin tuna were found to exhibit V-shaped profiles broadly across the North Atlantic, particularly in the open ocean connecting the identified putative foraging hotspots (Wilson & Block 2009), hence supporting the hypothesis of transiting behaviour as a function of Type 2 dives for large pelagic fish. However, in this study five blue sharks (out of six) exhibited descent rates higher than ascent in most of Type 2 dives. In particular, sharks S2 and S6 presented a very pronounced contrast. S6, the female tagged in the mid-Atlantic, performed a series of mesopelagic Type 2 dives with very high descent rates, in some cases up to 4.1 ms^{-1}. This is the opposite of what is proposed by the optimality models of diving behaviour mentioned above, underlining the high energetic demand of some of these Type 2 dives in the blue sharks of this study. Together with the fact that in some of the regions with high descent rates there was also observed a larger proportion of dives with intermediate to high intra-depth zone (IDZ) values, these Type 2 dives probably correspond to a strict exploratory behaviour. V-shaped dives with descent rates higher than the ascent have also been observed in blue (Carey & Scharold 1990) and

mako sharks (Sepulveda et al. 2004), tracked in the eastern North Atlantic and Pacific, respectively. In the case of mako sharks, these dives were frequently associated with feeding events (Sepulveda et al. 2004). It has been suggested that these fast descent and slower ascents might function as a method to visually detect prey individuals by silhouetting them against light from the surface (Carey & Scharold 1990). Nevertheless, the blue sharks tracked in this study frequently undertook dives below the photic zone, mostly within the mesopelagic realm but with some even into the bathypelagic one. As a result, such function of Type 2 dives does not seem to be a very likely explanation. Overall, blue sharks' Type 2 dives were mostly performed in off-shelf areas, associated with lower chlorophyll *a* concentrations. In one shark tagged off the European shelf, Type 2 dives were observed in a low productive area, connecting two regions with a very high proportion of prolonged Type 1 dives. Another shark presented Type 2 dives with very high descent rates and a larger proportion of intermediate to high intra-depth zone (IDZ) values in a very oligotrophic area. Therefore, the assumption that these dives correspond to transiting between foraging areas or an exploratory behaviour within a region with diffuse prey items seems to be consistent with the results obtained in this study. In Atlantic bluefin tuna, V-shaped profiles were typically observed linking presumed foraging hotspots, and from a study of stomach content analyses about 65 % of tunas caught in that region had empty stomach (Dragovich 1970), further supporting the proposed functions of Type 2 dives. Type 3 dives were defined in this study as being W-shaped, having between 2 to 4 wiggles around the maximum depth prior to the ascent. Overall, they occurred in higher proportion coupled with Type 2 dives (in the same lower productivity regions) and presented a depth distribution over the horizontal movements very similar to that class of dives in all sharks. This suggests that they might also function as travelling or exploratory dives, perhaps with a few feeding behaviours associated (that would create the wiggles in the bottom). Blue sharks are known to feed on several squid species, for example HISTIOTEUTHIDAE and OCTOPOTEUTHIDAE and including deep-water species as *Vampyroteuthis infernalis* and *Mastigoteuthis* sp. (N. Queiroz, unpublished data). Some of these species are often motionless or weakly swimming in the water column (e.g. Seibel et al. 1997). Consequently, blue sharks may be able to feed on such species while performing fast surveys through the water column. Type 4 dives consist of a V-dive with a 'stop' phase in the ascent. These dives have been described in literature analysing the diving profiles of green *Chelonia mydas* and loggerhead *Caretta caretta* turtles (Hochscheid & Godley 1999, Seminoff et al. 2006, Thomson et al. 2011). An additional type was observed in this study, Type 5 dives, and that are a mirror image of Type 4, having the 'stop' phase during the descent. It is worth noting that this shape of dives has been

represented graphically, namely in the diving profile of an elephant seal (Le Beouf & Laws 1994), but to our knowledge has not been labelled previously. In this study, these classes did not appear to be performed following a specific temporal pattern, with both types being generally interspersed within Type 1 and Type 2 dives (U- and V-shaped, respectively). In respect to their distribution along the horizontal movements of blue sharks, there was not a very congruent pattern. While some sharks exhibited these classes in frontal regions with enhanced primary production, others displayed them in off-shelf oligotrophic areas or even generally dispersed within their movements, in several types of habitats. The mean depth of the 'stop' phase in both Type 4 and 5 dives along blue sharks' horizontal movements was largely in accordance with the mean bottom phase depth of Type 1 dives in all individuals. It is possible that, in some regions, they might correspond to foraging on aggregated prey in a certain depth layer (similarly to Type 1 dives), hence the 'stop' phase, coupled with exploratory V-type events. However, the fact that they were generally observed in several different habitats does not seem to support this hypothesis. A significant positive correlation between the mean depth of the 'stop' phase and the maximum dive depth was detected in both classes of dives, for blue and also for basking sharks. In the case of Type 5 dives, which present the 'stop' during the descent phase, this may indicate that the sharks are anticipating the depth to which they will dive. Marine mammals and birds have been suggested to anticipate maximum dive depth based on correlations between descent rates or inhaled air volume (Otani et al. 1998, Sato et al. 2002). A correlation between the mean depth of the 'stop' phase and the maximum dive depth was also observed by Hochscheid & Godley (1999) in a green turtle dive type designated as 'S-dives' (that corresponds to the Type 4 designation of this study). The authors proposed that the 'stop' in the ascent would serve either as stationary mid-water resting or an energy conservation strategy of transiting turtles (Hochscheid & Godley 1999, Thomson et al. 2011), following a modelling study in fish swimming strategies (Weihs 1973). In the latter study, and in further investigations, it is suggested that individuals can optimize their costs of transport by taking advantage of their negative buoyancy and passively sink down to a certain depth, and then actively ascent to the surface (Weihs 1973, Videler & Weihs 1982, Williams et al. 2000, Hassrick et al. 2007, Gleiss et al. 2011). It is therefore possible that blue and basking sharks' Type 4 and 5 dives represent a similar energy conservation strategy. The sharks may be gliding during the 'stop' phase, optimizing their locomotory movements while travelling between prey patches or exploring new habitats.

4.2. Diel behaviour

The vertical distribution of blue sharks tagged in this study changed in a consistent fashion across each behavioural section, with three general patterns of diel depth distribution being observed in different individuals. Moreover, there were similarities in the frequency and proportion of time performing each type of dive among the six blue sharks when comparing between the behavioural sections with the same diel pattern of diving behaviour, as well as in the summary parameters assessed for each dive type.

Normal diel vertical migration with permanence at depth during daylight hours was observed in two individuals in this study, associated with stratified off-shelf waters, and also in blue sharks tagged in the northwest Atlantic, near the Gulf Stream (Campana et al. 2011). Such strong pattern of diel vertical movements has also been described in other marine predators (namely swordfish *Xiphias gladius* (Sedberry & Loefer 2001, Takahashi et al. 2003), bigeye tuna *Thunnus obesus* (Dagorn et al. 2000), bigeye thresher shark *Alopias superciliosus* (Nakano et al. 2003, Weng & Block 2004) and one megamouth shark *Megachasma pelagius* (Nelson et al. 1997)), and has been widely observed across the food chain down to zooplankton organisms (Hays 2003, Williamson et al. 2011). Diel vertical migration of zooplankton is generally characterized by organisms occurring at depth during daytime and shallower in the water column during the night. Several hypotheses have been advanced to account for these movements in zooplankton, being predator evasion the most supported one (Ohman et al. 1983, Bollens & Frost 1989, Hays 2003). Another nDVM pattern was observed in blue sharks in this study, which was also characterized by deeper depth occupation during the day when compared to night-time but with individuals spending a considerable amount of time at shallow waters during the day as well. On both cases, blue sharks' daytime depth was confined to a relatively narrow depth layer. In the North Atlantic Ocean, blue sharks are known to feed on vertically migrating prey items such as squids, hence such diel vertical migration patterns may be a strategy to maximize time spent at specific prey patches. Additionally, the sections where sharks exhibited nDVM were usually characterized by having days with several Type 1 dives (U-shaped), that comprised a very large proportion of diving time, and nights with very few dives, typically V-shaped (Type 2). A reverse DVM pattern, with daylight hours at the surface and night-time below the mixed layer, was also observed in weakly to well-stratified waters over the European shelf and near the shelf-edge. This reverse diel behaviour has been described in other elasmobranchs, including porbeagle *Lamna nasus* (Pade et al. 2009) and basking *Cetorhinus maximus* (Sims et al. 2005) sharks. Regarding the plankton-feeding basking shark, the reverse DVM pattern was observed in on-shelf

waters near the Ushant front, and was possibly related to an inversion of zooplankton DVM as an escape response from normal vertically migrating invertebrate predators (Sims et al. 2005). This basking shark behaviour was in fact induced by the predator-prey interactions of zooplankton and planktonic invertebrates. Similar interactions may be influencing blue sharks diel vertical migration, considering that blue sharks are probably tracking small pelagic fish and/or squid species, whose distributions are likely motivated by zooplankton aggregations. A surface-oriented behaviour, with no diel differences, was also observed in this study. In these behavioural sections the proportion of time spent performing each dive class was variable, with S1 displaying Types 1, 3 and 4 mainly by day at stratified shelf-break waters and Type 1 and 2 dives both at day and night when diving off-shelf. Other pelagic fish species have been observed displaying surfacing behaviours, for example basking (Sims, Southall, Merrett, et al. 2003) and salmon sharks *Lamna ditropis* (Carlisle et al. 2011), billfishes (e.g. white marlins, Horodysky et al. (2007)) and tunas (e.g. yellowfin tuna *Thunnus albacares*, Weng et al. (2009)). Most of the times it is not possible to obtain detailed records of prey abundances and distribution along with the horizontal and vertical movements recorded by electronic tags, however the mentioned study on basking sharks did have zooplankton samples and observed that the surface-swimming duration of basking sharks increased significantly with increasing minimum zooplankton density (Sims, Southall, Merrett, et al. 2003). Applied to blue sharks, the observed strong association with surface waters may indicate that prey densities may be high enough for them to remain foraging at surface waters throughout the day. Irregular diving behaviour, with frequent excursions into deep waters without a diel component, was observed in two sharks when in stratified deep oceanic waters. One was the blue shark tagged in the western North Atlantic, near Newfoundland and the Flemish Cap. In this region there is some level of mixing between the warm Gulf Stream current and the colder shelf-break Labrador Current (Fratantoni & Pickart 2007), and indeed the estimated thermocline depth was highly variable within each day, therefore probably resulting in irregular vertical movements across the section. The other irregular behaviour was observed in a highly oligotrophic region in the middle Atlantic, and may be a result of more complex search patterns for very disperse prey items. Overall, it appears that different diel vertical behaviours are exhibited by blue sharks in response to changes in prey type or availability, although in some cases blue sharks' behaviour may be directly related to the thermal structure of the water column, since it can influence the distribution of prey (Sims & Quayle 1998).

5. CONCLUSION

The two shark species considered in this study, blue *Prionace glauca* and basking *Cetorhinus maximus* sharks, presented high variability in the vertical movements recorded by satellite tags, both inter- and intra-individuals. Interesting, however, was the fact that in all individuals from the two species the majority of dives could be grouped in five main categories based on their two-dimensional (time vs. depth) shape. Furthermore, all but one of these types have also been described among other pelagic divers, from turtles, marine birds and mammals to a few fish species, supporting the hypothesis that they in general correspond to foraging behaviours, namely prey searching and feeding. Basking sharks are mega-planktivorous, being apex predators in a relatively short food chain (phytoplankton-zooplankton-vertebrate). At small spatial scales, they selective filter-feed on large zooplankton along oceanic and inner-shelf thermal fronts, or in areas that contain high zooplankton densities (Sims & Merrett 1997, Sims & Quayle 1998). It has also been observed that the duration of surface-swimming behaviour of basking sharks increased significantly with increasing minimum zooplankton densities (Sims, Southall, Merrett, et al. 2003). It is therefore reasonable to assume that the permanence at depth observed in basking sharks in this study, namely in the form of consecutive U-shaped dives (Type 1 and Types 1A to 1D), is likely a result of high densities of zooplankton aggregated in certain depth layers. Blue and basking sharks presented some similarities in the characteristics of these dive classes, for example Type 1 dives having extended durations and generally performed within a uniform depth in both species. These results highlight the usefulness and applicability of high-resolution dive profiles' analysis of pelagic predators, so that we can increase our understanding of their patterns of space use at finer

scales. By investigating differently shaped dive profiles combined with the general horizontal movements and the oceanographic gradients experienced by the individuals, we can identify areas with different habitat use, namely transiting and foraging grounds. This analysis may therefore provide a significant contribute to the identification of potential marine protected areas, particularly if integrating data from several species, in a time where pelagic predators are being severely exploited and a detailed knowledge of their behavioural ecology is still lacking, at least for some species. It is worth to note that there are several aspects related to the shape of dive profiles, namely horizontal path and acceleration within each dive, which cannot be examined when analysing archival data recorded by PSAT tags only. Moreover, considering as well that the oceans are a very heterogeneous environment, particularly regarding prey types and densities, it is possible that dives with apparently similar shapes can correspond to different activities. In fact, this was observed in green and loggerhead turtles, for which the dive shape analysis was complemented with video recordings (Seminoff et al. 2006, Thomson et al. 2011). Therefore, further approaches contemplating the analysis of high resolution dive profiles of pelagic predators to infer their functions, and consequently assess habitat use in different regions, should consider the inclusion of additional information that can help us to evaluate the reliability of those inferences.

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7. SUPPLEMENTARY MATERIAL

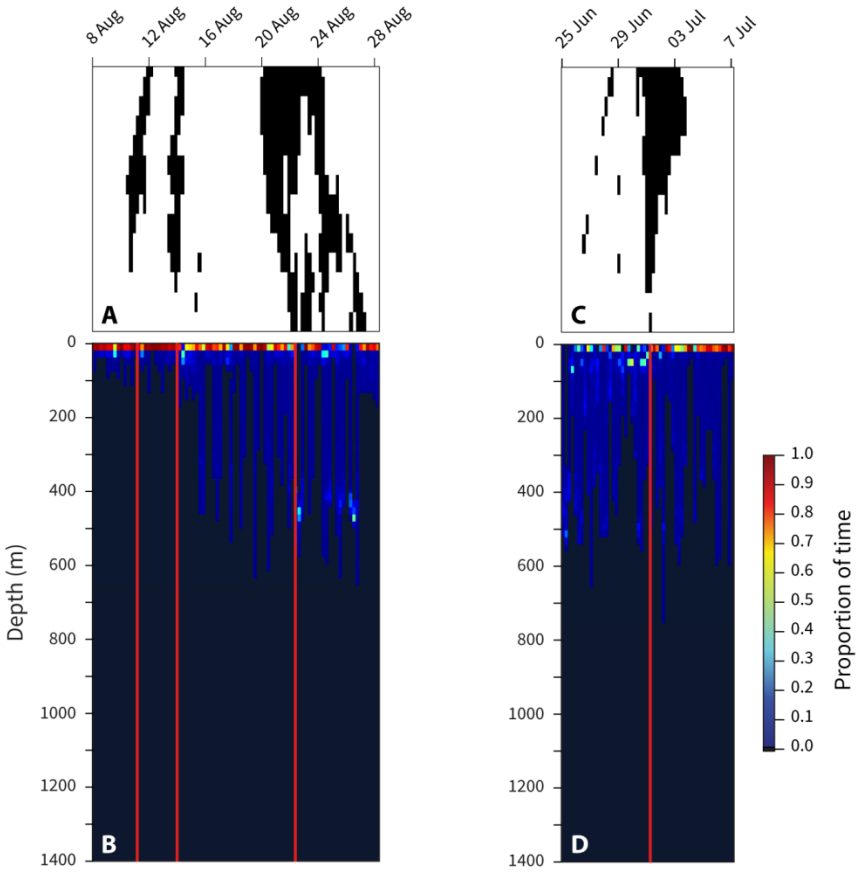

Fig. S. 1. Split-moving window result diagrams (A, C) and surface plot of time-at-depth (TAD) matrix (B, D) of blue sharks S2 (left panel), tagged off Plymouth, and S5 (right panel), tagged near Newfoundland. Significant discontinuities in the time series of vertical movements are depicted along the surface plot (vertical red lines).

Table S. 1. Start and ending dates of each behavioural phase identified for all individuals, using the Split-Moving Window analysis Basking sharks (S7 to S12), sections obtained by Humphries et al. (2010).

Shark ID	Section ID	Start date	End date
S1	SEC 1	2006-06-21 13:13	2006-07-30 09:00
	SEC 2	2006-07-30 09:00	2006-08-02 09:00
	SEC 3	2006-08-02 09:10	2006-08-10 12:39
S2	SEC 1	2006-08-08 10:08	2006-08-11 11:59
	SEC 2	2006-08-11 12:00	2006-08-14 11:59
	SEC 3	2006-08-14 12:00	2006-08-22 23:59
	SEC 4	2006-08-23 00:00	2006-08-29 06:00
S3	SEC 1	2007-08-01 11:23	2007-08-08 11:59
	SEC 2	2007-08-08 12:00	2007-08-14 05:04
S4	SEC 1	2007-08-24 10:36	2007-08-31 23:59
	SEC 2	2007-09-01 00:00	2007-09-22 23:59
	SEC 3	2007-09-23 00:00	2007-09-29 23:59
	SEC 4	2007-09-30 00:00	2007-10-08 23:59
	SEC 5	2007-10-09 00:00	2007-11-02 14:20
S5	SEC 1	2010-06-25 06:57	2010-07-02 11:59
	SEC 2	2010-07-02 12:00	2010-07-08 21:00
S6	SEC 1	2011-08-28 08:34	2011-09-03 23:59
	SEC 2	2011-09-04 00:00	2011-10-04 23:59
	SEC 3	2011-10-05 00:00	2011-10-14 23:59
	SEC 4	2011-10-15 00:00	2011-11-09 23:59
	SEC 5	2011-11-10 00:00	2011-11-30 10:52
S7	SEC 1	2001-05-24 00:00	2001-06-11 23:59
	SEC 2	2001-06-12 00:00	2001-06-30 23:59
	SEC 3	2001-07-01 00:00	2001-07-30 00:00
S8	SEC 1	2001-05-25 07:35	2001-06-29 23:59
	SEC 2	2001-06-30 00:00	2001-07-08 23:59
	SEC 3	2001-07-09 00:00	2001-12-04 12:51
S9	SEC 1	2001-07-31 08:04	2001-08-30 12:00
	SEC 2	2001-08-30 12:01	2002-02-10 16:25
S10	SEC 1	2001-08-02 03:43	2001-08-19 00:00
	SEC 2	2001-08-19 00:00	2001-08-31 00:00
	SEC 3	2001-08-31 00:00	2001-09-04 00:00
	SEC 4	2001-09-04 00:00	2001-09-08 00:00
	SEC 5	2001-09-08 00:00	2001-09-16 00:00
	SEC 6	2001-09-16 00:00	2001-09-19 15:03
S11	SEC 1	2002-06-18 00:00	2002-06-21 00:00
	SEC 2	2002-06-21 00:00	2002-06-25 00:00
S12	SEC 1	2004-06-01 08:46	2004-06-05 08:00
	SEC 2	2004-06-05 08:01	2004-06-22 23:59
	SEC 3	2004-06-23 00:00	2004-06-24 23:59
	SEC 4	2004-06-25 00:00	2004-07-03 00:00

Table S. 2. Offset values used for each shark to correct depth data from the pressure-sensor drift. * Individuals that presented negative depth readings.

Shark ID	Species	Offset value (m)
S1	*P. glauca*	1.5
S2	*P. glauca*	1.5
S3	*P. glauca*	3.5
S4	*P. glauca*	0 *
S5	*P. glauca*	4.5
S6	*P. glauca*	2.5
S7	*C. maximus*	0 *
S8	*C. maximus*	0 *
S9	*C. maximus*	0 *
S10	*C. maximus*	0
S11	*C. maximus*	0
S12	*C. maximus*	0 *

Table S. 3. Sunrise and sunset times estimated for each five-day interval of the blue sharks' tracking period, using the light level values recorded by the tags.

Shark ID	5-days interval	Sunrise	Sunset
S1	21/07 - 26/07	4:20	21:00
	27/07 - 01/08	4:30	20:40
	02/08 – 06/08	5:00	20:30
	07/08 – 10/08	5:15	20:15
S2	08/08 – 18/08	4:20	20:30
	19/08 – 29/08	5:00	20:15
S3	01/08 – 06/08	4:45	21:00
	07/08 – 11/08	4:45	21:00
	12/08 – 14/08	5:00	20:40
S4	24/08 – 29/08	4:45	20:00
	30/08 – 03/09	5:10	19:20
	04/09 – 08/09	5:10	19:10
	09/09 – 13/09	5:10	19:00
	14/09 – 18/09	5:25	19:00
	19/09 – 23/09	5:40	18:45
	24/09 – 28/09	5:40	18:45
	29/09 – 03/10	5:55	18:30
	04/10 – 08/10	6:05	18:20
	09/10 – 13/10	6:10	18:20
	14/10 – 18/10	6:10	18:05
	19/10 – 23/10	6:25	18:05
	24/10 – 28/10	6:25	17:50
	29/10 – 02/11	6:40	17:35
S5	25/06 – 08/07	6:40	23:20
S6	28/08 – 02/09	7:05	21:00
	03/09 – 07/09	7:05	20:55
	08/09 – 12/09	7:05	20:55
	13/09 – 17/09	7:20	20:25
	18/09 – 22/09	7:20	20:25

	23/09 – 27/09	7:20	20:05
	28/09 – 02/10	7:20	20:05
	03/10 – 07/10	7:20	20:00
	08/10 – 12/10	7:20	19:45
	13/10 – 17/10	7:20	19:45
	18/10 – 22/10	7:25	19:30
	23/10 – 27/10	7:25	19:30
	28/10 – 01/11	7:25	19:30
	02/11 – 06/11	7:25	19:30
	07/11 – 11/11	7:35	19:15
	12/11 – 16/11	7:35	19:15
	17/11 – 21/11	7:35	19:15
	22/11 – 26/11	7:35	19:15
	27/11 – 30/11	7:35	19:15

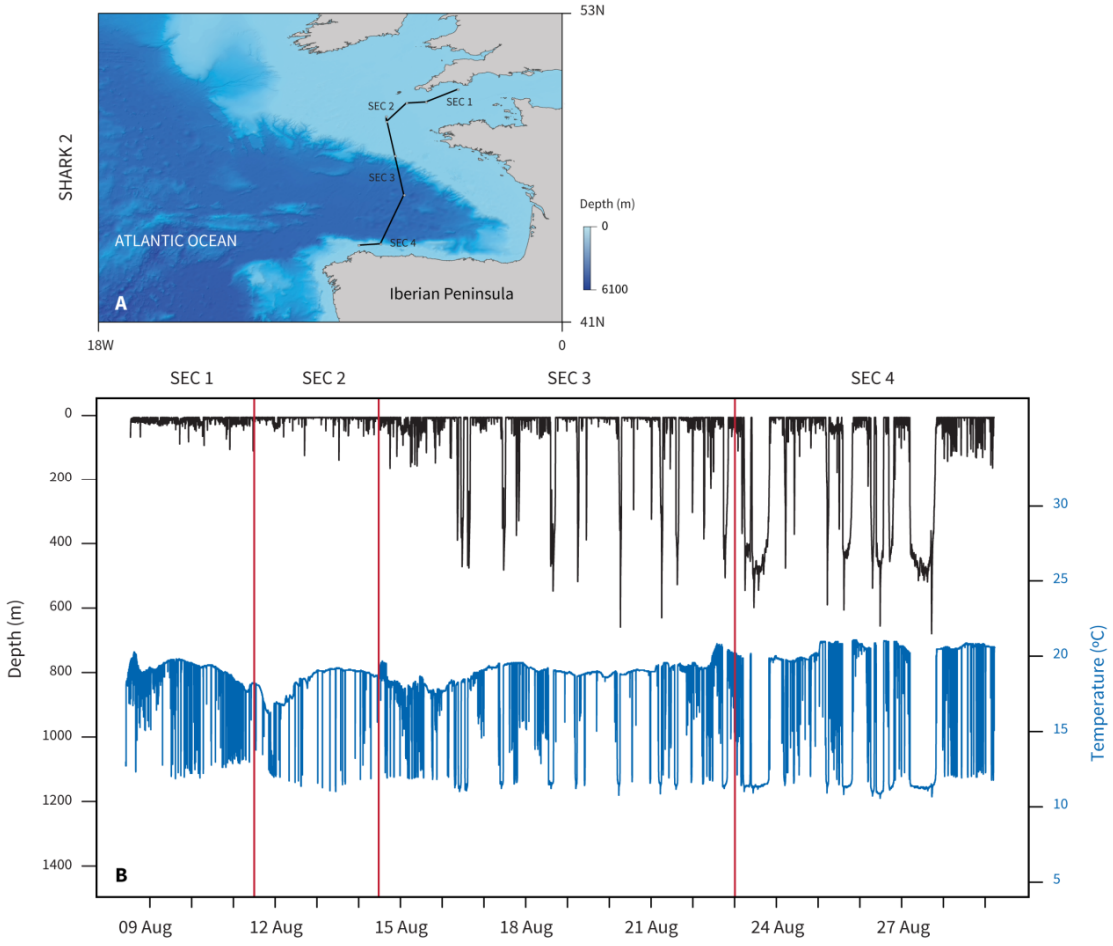

Fig. S. 2. Depth (black) and water temperature (blue) high-resolution profiles (B) of shark S2, tagged near the English Channel (A). Vertical red lines correspond to significant shifts in depth occupation and where the depth time series was divided into sections ('SEC') following the results of the Split-Moving Window analysis.

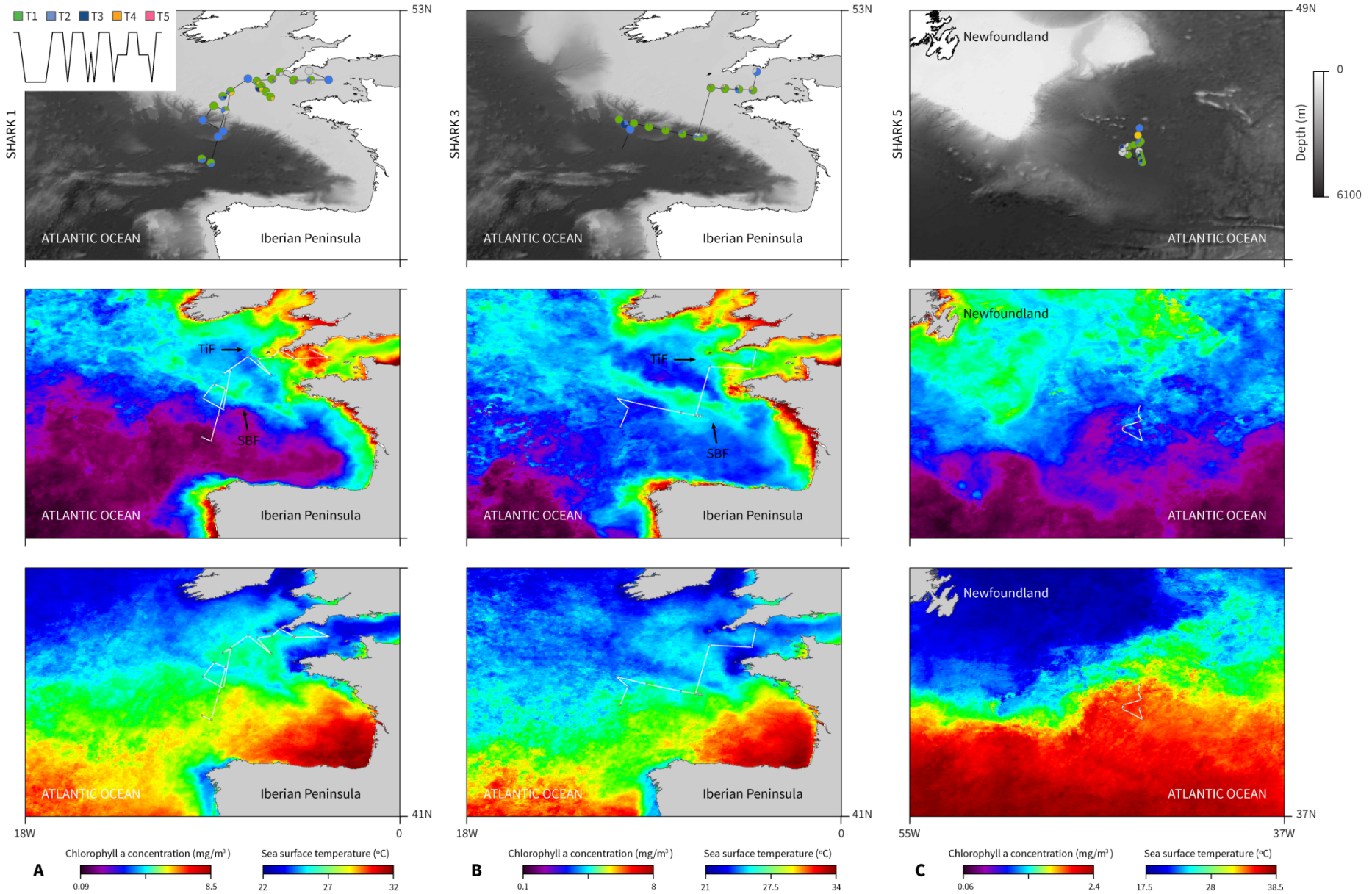

Fig. S. 3. Dive classes of three blue sharks represented along their horizontal movements and relation with oceanographic gradients. General movement patterns of sharks S1 (A), S3 (B) and S5 (C), with pie charts of daily proportion of time spent performing each dive type (top panels) and tracks overlaid on seasonal average of chlorophyll *a* concentration (middle panel) and sea surface temperature (bottom panels). TiF: tidal induced front; SBF: shelf-break front; WS UpF: Western Sahara upwelling front.